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The Deuterium Balance of Lake Maracaibo[1]

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ABSTRACT

A balance sheet for the gains and losses of deuterium from Lake Maracaibo, using estimates based on climatological data for the exchanges of water and measurements of the deuterium content of lake water, rainfall, river flow, and Caribbean Sea water to obtain the volumes of the deuterium exchange, indicates that the relations are qualitatively satisfactory, although not numerically exact.

The concentration of deuterium, present chiefly as HDO, differs in various natural waters (Friedman 1953). Deuterium consequently promises to provide a tracer useful in the study of the water cycle of the earth. The differences are presumed to arise from the different vapor pressures of H_2O and HDO which cause fractionation when natural waters evaporate, from the differential behavior of these water substances in the condensation of rain or snow, and from the mixing of waters of different deuterium content in the sea or elsewhere.

Lake Maracaibo provides a favorable situation in which to compare the deuterium content of the intercommunicating waters and thus to examine the theory of the physical relations responsible for the deuterium cycle in nature. The lake lies in a watershed sharply delineated by mountains, its hydrography is adequately known, water balance has been deduced from analysis of the climatological data, and analyses of the deuterium content of samples of the natural waters involved have been made. The combined data available from these sources permit a tentative balance sheet to be drawn for the lake, and thus permit a critical scrutiny of the factors on which the balance seems to depend.

The hydrography has been studied by the Woods Hole Oceanographic Institution, working under contract with the Creole Petroleum Corporation. This study confirms and extends the earlier observations of Gessner (1953). The climatological data have been analyzed by Carter, employing methods outlined by Thornthwaite (1948), to obtain estimates of the mean annual runoff from the watershed, rainfall on the lake, and evaporation from its surface. Consideration of the salt content of lake water allowed the water balance to be completed by the addition of estimates of the inflow of sea water and the outflow of lake water into the Caribbean Sea. Deuterium

[1] Contribution Number 867 from the Woods Hole Oceanographic Institution. Publication authorized by the Director of the U. S. Geological Survey.

TABLE 1. *Analyses of deuterium in natural waters of and adjacent to Lake Maracaibo*

Station	Date	Latitude °N.	Longitude °W.	Depth ft	Temperature °C	Chloride ppm	Deuterium mole per cent
			Lake Maracaibo				
87	Mar. 24, 1954	9°17′	71°12′	1	29.80	638	0.01527
87	Mar. 24, 1954	9°17′	71°12′	15	29.51	642	—
87	Mar. 24, 1954	9°17′	71°12′	20	29.53	638	—
87	Mar. 24, 1954	9°17′	71°12′	40	29.48	650	0.01527
87	Mar. 24, 1954	9°17′	71°12′	55	29.46	633	0.01527
70	Mar. 18, 1954	9°24′	71°43′	10	29.31	735	0.01529
70	Mar. 18, 1954	9°24′	71°43′	42	29.42	732	0.01527
70	Mar. 18, 1954	9°24′	71°43′	63	29.27	720	0.01526
72	Mar. 19, 1954	9°40′	71°35′	10	29.07	756	0.01521
72	Mar. 19, 1954	9°40′	71°35′	21	28.97	760	0.01526
72	Mar. 19, 1954	9°40′	71°35′	63	28.62	835	0.01529
72	Mar. 19, 1954	9°40′	71°35′	74	28.54	1,039	0.01527
72	Mar. 19, 1954	9°40′	71°35′	84	28.52	1,110	0.01527
11	May 30, 1953	9°44′	71°14′	10	31.16	690	0.01521
21	Jun. 1, 1953	9°44′	71°43′	1	30.55	670	0.01518
21	Jun. 1, 1953	9°44′	71°43′	98	28.52	1,540	0.01523
90	Mar. 3, 1954	9°46′	71°38′	60	28.49	1,312	0.01530
90	Mar. 3, 1954	9°46′	71°38′	88	28.39	2,020	0.01527
80	Mar. 23, 1954	9°55′	71°21′	1	29.80	720	—
74	Mar. 19, 1954	9°56′	71°27′	1	29.84	740	—
74	Mar. 19, 1954	9°56′	71°27′	10	29.59	735	—
74	Mar. 19, 1954	9°56′	71°27′	21	29.07	732	—
74	Mar. 19, 1954	9°56′	71°27′	53	28.99	731	—
74	Mar. 19, 1954	9°56′	71°27′	63	28.96	749	—
74	Mar. 19, 1954	9°56′	71°27′	86	28.81	1,009	—
10	May 30, 1953	10°02′	71°26′	1	31.00	670	0.01513
10	May 30, 1953	10°02′	71°26′	20	30.11	660	0.01516
10	May 30, 1953	10°02′	71°26′	40	29.44	665	0.01518
10	May 30, 1953	10°02′	71°26′	80	29.42	660	0.01520
10	May 30, 1953	10°02′	71°26′	98	29.12	1,265	0.01520
79	Mar. 3, 1954	10°07′	71°24′	1	29.80	684	—
94	Mar. 27, 1954	10°10′	71°22′	1	29.74	670	—
9	May 30, 1954	10°20′	71°36′	1	30.13	670	0.01523
			Strait of Maracaibo and Channel				
28	Mar. 14, 1954	10°26′	71°34′	39	27.37	8,340	0.01542
76	Mar. 22, 1954	10°42′	71°34′	5	28.14	2,160	0.01536
76	Mar. 22, 1954	10°42′	71°34′	15	28.16	2,535	0.01533
76	Mar. 22, 1954	10°42′	71°34′	25	27.75	4,190	0.01532
76	Mar. 22, 1954	10°42′	71°34′	35	27.05	8,710	0.01542
76	Mar. 22, 1954	10°42′	71°34′	42	26.94	14,700	0.01548
5	May 27, 1953	10°48′	71°38′	1	30.02	840	0.01521
8	May 28, 1953	10°59′	71°36′	1	30.06	2,800	0.01529
			Gulf of Venezuela				
5239	Dec. 8, 1954	11°09′	71°46′	1	27.32	7,130	0.01524
5239	Dec. 8, 1954	11°09′	71°46′	9	27.78	14,650	0.01542
5240	Dec. 8, 1954	11°19′	71°43′	1	27.56	13,210	0.01542
5240	Dec. 8, 1954	11°19′	71°43′	19	28.16	18,080	0.01546
5245	Dec. 8, 1954	11°28′	71°06′	1	27.87	16,706	0.01545
5245	Dec. 8, 1954	11°28′	71°06′	13	28.02	18,190	0.01544
5242	Dec. 8, 1954	11°38′	71°40′	1	27.63	9,320	0.01531
5242	Dec. 8, 1954	11°38′	71°40′	8	27.74	13,100	0.01540
5251	Dec. 9, 1954	11°58′	70°44′	1	27.22	19,630	0.01545
5251	Dec. 9, 1954	11°58′	70°44′	50	25.43	20,140	0.01548
5237	Dec. 7, 1954	12°19′	69°56′	1	27.56	19,710	0.01545
5237	Dec. 7, 1954	12°19′	69°56′	99	22.00	20,360	0.01551
5256	Dec. 9, 1954	12°34′	71°01′	1	27.35	19,750	0.01547
5256	Dec. 9, 1954	12°34′	71°01′	65	23.49	20,310	0.01543
	Mar. 30, 1954	10°30′	68°3′	1	—	20,340	0.01550

analyses were made at the U. S. Geological Survey using methods described by Friedman (1953). The results are expressed as mole per cent HDO/H_2O and are believed to be accurate to at least 0.00015 mole per cent which is 1% of the quantity usually present. Samples of rain water were obtained through the courtesy of Mr. Earlston Doe of the Creole Petroleum Corporation.

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LAKE WATER

The volume of the lake when divided by the estimated mean annual outflow indicates that the water remains in the lake about ten years. The chloride content shows that the lake water is a mixture of 1 part of sea water and 30 parts of fresh water; this provides an index of its homogeneity. The water is thoroughly mixed vertically to the bottom at depths of 100 feet, except for a relatively limited pool of more saline water over the bottom near the center of the basin. Otherwise the water is nearly homogeneous in all parts because of a rapid, cyclonic circulation.

The deuterium content of 23 scattered samples of lake water is recorded in Table 1. It has a mean value of 0.01525 mole per cent, the individual measurements ranging from 0.01513 to 0.01530. No significant difference can be detected between samples from different parts of the lake nor from different depths. The representative deuterium content of lake water is 0.0152 mole per cent.

EXCHANGE WITH THE SEA

The water lost to the sea is lake water to which a deuterium content of 0.0152 has

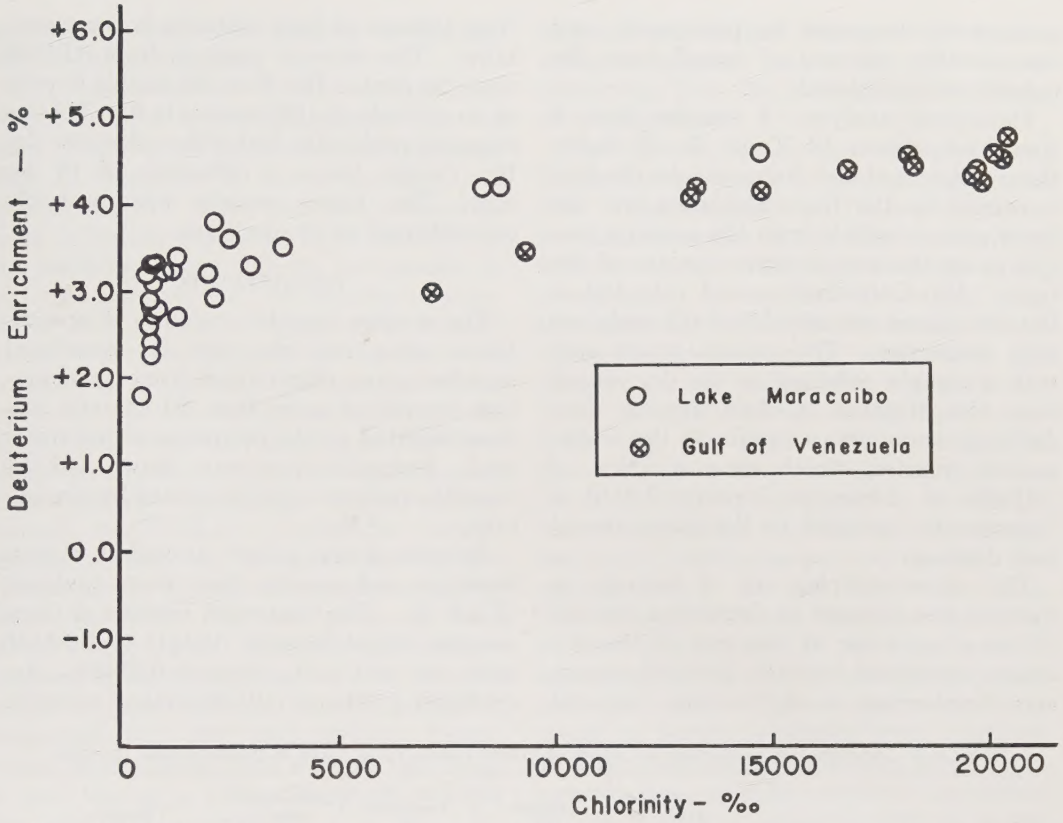

FIG. 1. Relation of deuterium content and chloride content of water samples from Lake Maracaibo and the Gulf of Venezuela.

been assigned. A relatively small quantity of sea water of Caribbean origin enters the lake, chiefly during the dry season (in winter) to provide the observed chloride content. Caribbean water, sampled off the approaches to the Gulf of Venezuela, has a deuterium content of 0.01550.

In the Strait of Maracaibo, in the inner part of the Gulf of Venezuela, and in the connecting channel across Tablazo Bay, mixtures of lake water and Caribbean water are found in various proportions. Figure 1 shows the relation between the chloride content and the deuterium content of water samples from this region. The linear relationship indicates that the varied deuterium content is the simple result of physical admixture of the two source waters.

LAND DRAINAGE

The Maracaibo basin varies from semiarid desert along the coast to tropical rain forest along the southern margin of the lake. The surrounding mountains rise to elevations of 15,000 feet above sea level. Much of the area is inaccessible and unsettled, and consequently the integration of the climatic factors determining the water balance of the uplands was difficult. Records were available of temperatures from 23 stations and of precipitation from 68 stations for varying periods.

From these data an accounting of the monthly gains, losses, and storage of moisture at each climatological station was made according to the procedures devised by Thornthwaite and his associates.[2] The estimated monthly values of runoff obtained by the method were mapped, using altitude as a guide to the distribution. The map

[2] The basic method is described by Thornthwaite (1948); however, the method has since been modified and presented in relation to its applications in Thornthwaite and Mather (1955).

areas were integrated by planimetry, and the monthly volumes of runoff from the upland were computed.

Deuterium analyses of samples from 8 rivers are shown in Table 2. Probably three-quarters of the drainage into the lake is carried by the Rio Catatumbo and the lesser streams which drain the swampy jungles along the southwestern quarter of the basin. Rio Catatumbo water collected in the wet season contained 0.01461 mole per cent deuterium. This value agrees well with a sample collected in the dry season from Rio Motatan, a clear running river draining mountainous terrain in the southeastern quarter, which gave a value of 0.01468. A deuterium content 0.0146 is consequently assigned to the mean annual land drainage.

The other samples are of interest in showing the increase in deuterium content of the river water at the end of the dry season northward into the semiarid region, and the decrease in the samples collected from streams at high altitudes in the mountains. The extreme range is from 0.01393 mole per cent in Rio Poco del Aquila flowing at an altitude of 4130 meters to 0.01572 in a stagnant pool in the bed of the otherwise dry Rio Pueblo Viejo, a difference of 13 per cent. The latter sample was probably concentrated by evaporation.

PRECIPITATION

The average monthly volumes of precipitation onto the lake and its associated marshes were determined from precipitation records at more than 20 climatic stations situated on the periphery of the water area. Isohyetal maps were drawn and the monthly volumes were integrated by planimetry.

Samples of rain water collected at various locations and seasons have been analyzed (Table 2). The deuterium content of these samples varied between 0.01411 and 0.1546 mole per cent and averaged 0.01495. Accordingly a value of 0.0150 is taken as repre-

TABLE 2. *Analyses of deuterium in water of rivers tributary to Lake Maracaibo and in rain*

	Date	Latitude °N.	Longitude °W.	Deuterium mole per cent	Remarks
		River water			
Rio Catatumbo	May 31, 1953	9°19.5′	71°47′	0.01461	4 miles above mouth
Rio Motatan	Mar. 29, 1954	9°38′	70°43′	0.01468	running freely
Rio San Juan	Mar. 29, 1954	9°45′	70°50′	0.01479	running freely
Rio San Piedro	Mar. 29, 1954	9°52′	70°53′	0.01495	scarcely flowing
Rio Pueblo Viejo	Mar. 29, 1954	10°02′	71°10′	0.01572	stagnant pool
Rio Merida	Feb. 3, 1956	Trib. of Rio Escalante		0.01460	2,000 meters altitude
Rio Poco del Aquila	Apr. 9, 1955	Near divide between Maracaibo and Orinoco		0.01393	4,130 meters altitude
Rio Poco del Aquila	Feb. 4, 1956	Near divide between Maracaibo and Orinoco		0.01397	4,130 meters altitude
Rio La Mesa	Apr. 9, 1955	Rio Motatan system		0.01437	1,800 meters altitude
Rio La Mesa	Apr. 9, 1955	Rio Motatan system		0.01416	3,000 meters altitude
		Rain water			
Off Santa Maria	Sep. 20, 1955	9°05′	71°22′	0.01411	
Central Lake Maracaibo	Mar. 25, 1954	9°27′	71°22′	0.01546	heavy shower
Off La Ceiba	Dec. 1, 1955	9°29′	71°06′	0.01452	
La Salina	Apr. 25, 1955	10°23′	71°27′	0.01524	
La Salina	Aug. 15, 1955	10°23′	71°27′	0.01509	
La Salina	Sep. 16, 1955	10°23′	71°27′	0.01515	
La Salina	Jan. 3, 1956	10°23′	71°27′	0.01516	
Maracaibo	Jun. 29, 1955	10°39′	71°37′	0.01483	

senting the deuterium content of average rain falling on the lake.

The interpretation of the variable deuterium content of the rain samples requires some review of the physics of the fractionation of deuterium in the evaporation and precipitation of water and of the observations in nature that may be interpreted by the resulting theory. It can be expected on physical grounds that the moisture evaporated from a water surface will contain about 6 per cent less deuterium than the source water (Epstein, Friedman, and Urey, in press). If evaporation and precipitation are strictly reciprocal aspects of the fractional distillation process, the *initial* precipitate from air immediately over the water surface should have a deuterium content similar to that of the source water. The precipitate, however, will contain relatively more deuterium than the moist air from which it separates. Consequently the remaining moisture in the air will be left with relatively less deuterium than the original evaporate from the water surface. Subsequent precipitation from such air will yield a rain having a lower deuterium content than the initial precipitate.

The expectations raised by these considerations are that rain precipitated from air immediately over the sea will have a deuterium content similar to the surface sea water, whereas that precipitated at higher altitudes, during the later stages in the ascent of air in convective rain storms, in the course of the ascent of moist air over mountains, or after a long period of drift across continental masses, will have lower deuterium content.

These expectations are supported by observations made in Hawaii where it was found that rain collected near sea level approached the surface sea water in deuterium content, whereas that collected at higher altitudes contained a smaller quantity, 0.0003 mole per cent less (Friedman and Woodcock, in press). Substantial evidence has also accumulated from the analysis of ice from mountain glaciers and of other natural waters at high altitudes that the precipitation at altitude has a low deuterium content. In contrast, river water from the southeastern United States yields higher values compatible with a relatively immediate origin from the precipitation of gulf air (Friedman 1953).

The variable deuterium content of the Maracaibo rains can be interpreted as follows. The samples from La Salina, at the seaward extremity of the lake, (content $\simeq$ 0.0152 mole per cent) represents the initial precipitation of maritime air derived from the Caribbean (surface deuterium $\simeq 0.0154$). A similar origin may be assigned to the sample from the central lake, which was obtained at a period when strong trade winds blew into the basin. The contribution that moisture evaporated directly from the lake's surface may have made to these rains cannot be assessed since the lake water contains only 0.0002 mole per cent less than the surface water of the Caribbean. The samples from off Santa Maria and La Cieba, at the southern end of the lake, contain substantially less deuterium (0.0141–0.0145 mole per cent). These samples are interpreted as having originated from maritime air after depletion in deuterium by previous precipitation, either as a result of convection to high altitude or a longer history of movement over the continent. The low value of the Maracaibo specimen may be similarly explained.

It should be noted that the low deuterium content of the samples from Santa Maria and La Cieba approaches the low values obtained from mountain streams at altitudes of 3,000–4,000 meters in the nearby mountains. The fact that the average value of the deuterium content assigned to the land drainage, based on analyses of river waters, is lower than the average value assigned to the lake rain seems to arise from the preponderance of rainfall of low deuterium content over the southern part of the Maracaibo drainage basin.

It is clear that much more detailed information on the origin and movements of the air masses which occupy the Maracaibo basin, of the deuterium content of their contained moisture and the mechanisms by which it is precipitated is required before the data on the deuterium content of the rainfall into the lake can be evaluated so as

to provide an accurately weighted mean value. The attribution of 0.0150 mole per cent to the rainfall on the lake is unsatisfactory but is made in lieu of a more certain figure.

EVAPORATION

Monthly averages of evaporation and evapotranspiration were estimated for each climatological station near the shore of Lake Maracaibo and its marshes. From monthly maps of this distribution, the average loss from the lake was reckoned by the same methods used in estimating precipitation over the lake.

The deuterium content of the evaporate is estimated from physical considerations to be 6 per cent less than that of the lake water, or 0.0143 mole per cent (Epstein, Friedman, and Urey, in press).

THE BALANCE SHEET

Table 3 gives the tentative balance sheet for the mean annual gains and losses of ordinary water and deuterium for Lake Maracaibo.

The items for the water balance are based on the climatological estimates. These estimates are not considered very precise, and it should be noted that the perfection of the balance is the result of estimating the loss to the sea from the difference between the gains and the evaporation, there being no independent measure of this loss.

The source of the deuterium concentration assigned to the items and their reliability have been discussed. The quantities of deuterium in the items are obtained by multiplying the quantity of water by the moles per cent deuterium $\times 10^{-2}$.

The gains and losses in deuterium agree to about 1 per cent. This is of the same order of accuracy as the individual deuterium determinations. When it is considered that the total deuterium concentrations do not differ among themselves by more than 8 per cent, and that the water balance has an arbitrary perfection, this agreement is not as impressive as it seems. All that is claimed is that the various estimates and measurements fall together in a consistent and theoretically reasonable relationship.

TABLE 3. *Tentative balance sheets, Lake Maracaibo*

Gains	Water balance $10^9 m^3$/yr.	Source	HDO	
			Concentration mole per cent	Quantity $10^7 m^3$/yr.
Land drainage	32.2	Rio Catatumbo	0.0146	0.470
Rainfall	22.0	Lake rain	0.0150	0.330
Sea water	.7	Caribbean Sea	0.0155	0.011
	54.9			0.811
A. Losses				
To sea	22.0	Lake Maracaibo	0.0152	0.335
Evaporation	32.9	Physical estimate	0.0143	0.470
	54.9			0.805
B. Losses—adjusted to obtain deuterium balance				
To sea	28.0	Lake Maracaibo	0.0152	0.426
Evaporation	26.9	Physical estimate	0.0143	0.385
	54.9			0.811

Of the deuterium concentrations, the value assigned to rainfall is the most questionable. A large number of collections in time and position would be necessary to fix this value with greater certainty.

Permissible adjustments in the values of the water balance items would serve to correct the discrepancy in the heavy water balance. In the lower part of Table 3 the losses have been re-estimated so as to secure a balance of deuterium by readjusting the estimates of evaporation. The evaporation must be reduced by 18 per cent with a compensating increase in the loss to the sea to bring the items into balance. Smaller adjustments more generally applied would serve the same purpose and would be permitted by the precision of the estimates, but there is no rational basis for making such adjustments.

DISCUSSION

The deuterium balance and the water balance provide complimentary procedures for estimating our hydrologic economy. Although the physical processes that determine the circulation of H_2O and of HDO in nature are the same, differences in the physical properties of these molecules are sufficient

to cause recognizable differences in natural waters, which depend upon their history and which could not be detected otherwise. This important fact is illustrated by the discussion of the origin of the Maracaibo rains. The purpose of this paper will be met if, in spite of the admitted limitations of its conclusions, it draws attention to the value of deuterium as a tool for examining the natural processes on which the distribution and behavior of natural waters depend.

It is obvious that for technical reasons the deuterium cycle cannot be examined separately from the water cycle, and the results would be of minor interest if it could.

Lake Maracaibo has provided a promising water mass for the present study, not only because information is available on its hydrography and water balance but because its volume is sufficient relative to its water exchange to justify the use of long-term averages in estimating the balance of water movement. It should be pointed out, however, that the balances are shifting, both seasonally and over the years.

Records extending over 20 years show that the chloride content of the lake water increased gradually from 425 ppm in 1938 to a maximum of nearly 1200 ppm in 1948. Since that time the chlorides have diminished and at present approximate the earlier value. There are substantial reasons to believe that these changes were due to variation in the accessions of fresh water as rainfall and runoff. The data used in estimating the water balance for the lake, however, represent fairly the average over this period.

The Maracaibo basin experiences a marked annual cycle of precipitation. From January through April, when northeast trade winds thoroughly permeate the Lake Maracaibo basin, there is a general reduction in rainfall. During the remainder of the year, when the Maracaibo basin is a meeting place for air streams from the Caribbean and the interior of the continent, the wet season occurs. The effect of the seasonal variation in rainfall on the water balance of the lake is illustrated in Table 4. The rate of gain of water by runoff and precipitation is greatly increased during the wet season and is balanced by increased losses of lake water to the sea. The return of water to atmosphere by evaporation is little changed by the season. During the dry season evaporation exceeds the gains that depend on rainfall, and a net inflow of sea water into the lake results. Consequently there is a reversing movement of water to and from the atmosphere in the course of the year that is not brought out by the annual water balance.

TABLE 4. *Tentative water balance sheets for the months of dry and wet season, expressed as the mean monthly gain and loss averaged for the periods January through April, and May through December, respectively*

	Dry season $10^9 m^3$/month	Wet season $10^9 m^3$/month
Gains		
Runoff	1.078	3.488
Precipitation	1.125	2.188
Inflow	0.579	0
Total	2.782	5.676
Losses		
Evaporation	2.578	2.820
Outflow	0.205	2.856
Total	2.783	5.676

The gains and losses in deuterium must vary in a similar way with the season. They cannot be calculated in the absence of data on the seasonal changes in the deuterium content of the several items.

The Maracaibo basin provides an excellent example of the great significance of the atmospheric transport of moisture. During the dry season evaporation persistently exceeds precipitation, and moisture is lost from the basin by the transport of moisture in the atmosphere. Even in the wet season there are many times when precipitation over the basin is less than evaporation, although the excess precipitation during the whole period is so great that as much as half the precipitated water reaching the lake is returned directly to the sea. It is likely that both the total water and the deuterium which enter the basin and leave it as vapor without being precipitated are a much larger quantity than all that enters into the cycle of exchange revealed by the balance of the lake itself.

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The Heat Budget of a Body of Water of Varying Volume[1]

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ABSTRACT

When the heat budget is applied to determine the evaporation from a lake of varying volume, the water budget must be considered. Using the continuity of the system a modified equation for evaporation from the heat budget has been developed. The modified equation has a term in the denominator that includes a base temperature used in the calculations. This equation is flexible in use and permits minimizing errors due to unknown quantities in the water budget.

INTRODUCTION

The heat budget is a useful tool in both meteorology and oceanography. In meteorology it has been used to examine the radiative balance of the atmosphere at different latitudes, thereby determining the amount of heat necessary to be transported across a given latitudinal zone. In oceanography it has been used primarily to study evaporation from the ocean or regions thereof. In the past few years the heat budgets at Lake Mead and Lake Hefner have been studied to determine evaporation. This paper will review the method of applying the heat budget to determine evaporation from a lake, with the main emphasis restricted to a discussion of those terms whose evaluation is affected by the fact that we are dealing with a body of water of varying volume. Detailed applications of the heat budget are given by Anderson and Pritchard (1951) and in the Technical Report of the Lake Hefner Studies, U. S. Geological Survey (1954).

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THE HEAT BUDGET

The heat budget for the ocean or a lake is a statement of the first law of thermodynamics for an incompressible fluid. It states merely that "the rate of change of internal energy of the system is equal to the net flux of heat through the boundaries of the system."

A view of a hypothetical lake (Fig. 1) will indicate some of processes operating to change the internal energy of the lake or any selected body of water.

The internal energy is represented by the temperature structure of the lake. The change in this temperature structure during any given period is commonly referred to as the "heat storage" term of the heat budget.

At the surface heat is supplied to the lake by the incoming short-wave radiation from the sun and sky. If this radiation is measured by an Eppley pyrheliometer these observations must be corrected for reflection at the surface by measurement or by computation from the parameters of wind speed, sun angle, and cloud cover.

The long-wave radiation leaving the surface can be determined from the surface temperature and the emissivity of the water surface. The emissivity appears to be practicably independent of temperature and salinity, and to have a value of about 0.97 (U.S.G.S. 1954). The atmosphere in turn radiates long-wave radiation to the water surface. A Gier and Dunkel flat plate radiometer which is shielded on the bottom gives total incoming radiation, and used with Eppley pyrheliometer observations will reveal the incoming long-wave radiation. The difference between the calculated long-wave radiation leaving the water surface and the observed incoming long-wave

[1] U. S. Navy Electronics Laboratory Contributions Number 41. Paper presented at National Meeting, East Lansing, Michigan, September 1955.

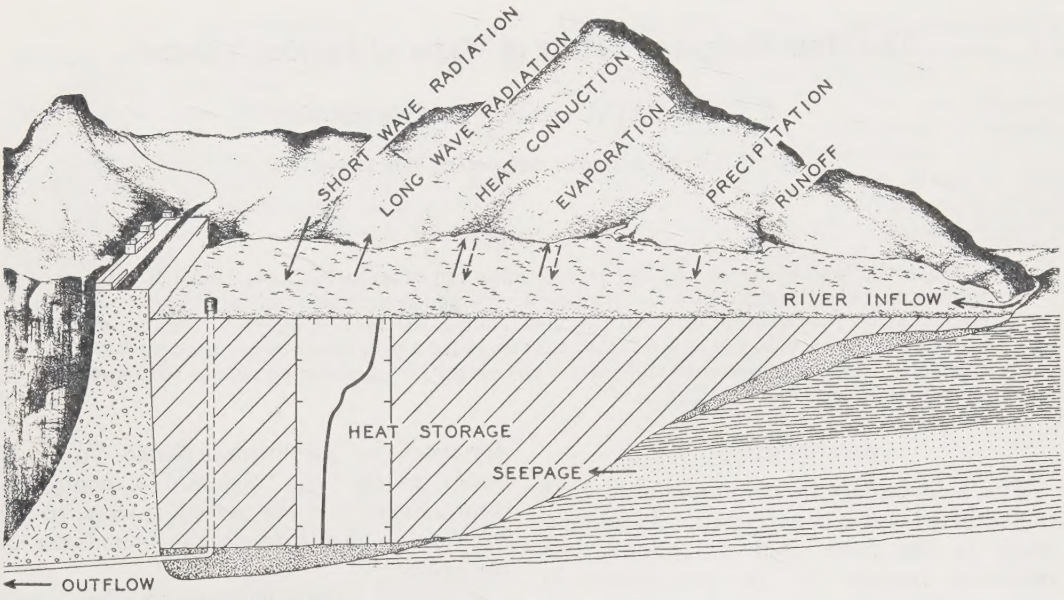

FIG. 1. Major heat exchange processes operating on a lake

radiation is the "net long-wave radiation" (sometimes called net "back" radiation) from the surface.

Heat is conducted away from (or towards) the water surface by contact of the air with the water surface. This "heat conduction" is related by measurements of temperature and humidity gradients above the surface to the heat used in the process of evaporation. This ratio of heat conduction to heat loss by evaporation is commonly called the "Bowen ratio."

A river flowing into the lake (or ocean currents in a region of the ocean), the outflow at the dam, bank run-off, precipitation, and seepage account for transportation of heat into or out of the lake. The net of these terms is the "advection" term in the heat budget.

Thus, the heat budget as applied to a body of water is usually expressed as

$$Q_\vartheta = Q_s - Q_b - Q_h - Q_e + Q_v \quad (1)$$

where for a selected time interval

Q_ϑ = change of heat stored in the body of water
Q_s = heat added by short-wave radiation
Q_b = heat lost by net long-wave radiation
Q_h = heat lost by conduction to the atmosphere
Q_e = heat lost by the process of evaporation
Q_v = heat added by advection.

Processes accounting for change in thermal energy which are neglected because of their small magnitude are:

1. conduction of heat through the bottom from the earth's interior
2. transformation of kinetic energy into heat
3. heating (or cooling) due to chemical processes
4. heating due to biological activity.

APPLICATION OF THE HEAT BUDGET

Prior to 1950 the heat budget was applied to special cases because of the difficulties encountered in evaluating the advected heat or the rate of change in heat storage. For example, Schmidt (1915) could neglect the advected heat and change in heat storage in considering evaporation from the oceans as a whole. Sverdrup *et al.* (1946) could compute the average annual values of evaporation at different latitudes in the Atlantic by assuming the net advection of heat by ocean currents was negligible. Richardson (1931) investigated evaporation from California lakes during time intervals when the change in air temperature was

small and assumed correspondingly negligible change in heat storage.

Preliminary studies on the monthly evaporation at Lake Mead by Anderson and Pritchard (1951) were followed by more detailed investigations of evaporation from lakes at Lake Hefner (U. S. Geological Survey 1954) and at Lake Mead (U. S. Geological Survey, in press) where the heat budget was one of the methods used. In such detailed investigations it is not possible to select only those time intervals, or conditions, whereby certain terms of the heat budget can be neglected. Each term must be evaluated for each given time interval. The Lake Hefner studies indicate that the heat budget can be applied to periods of one week or longer for computing evaporation, but loses accuracy for periods less than one week (USGS 1954). The assumptions and approximation that are made in the development to follow are those which experience has shown can be expected to hold for periods of one week to one month.

An examination of the heat budget equation shows that there are two types of processes for the heat transfer which must be evaluated. The first type does not require transfer of mass—non advective processes—and includes incoming short-wave radiation, outgoing long-wave radiation, and heat conduction. In the second type the heat is carried into and out of the system by an exchange of mass. This includes evaporation. Also the computation of heat storage falls into the latter class, inasmuch as it involves change of heat in a changing mass. It is the computation of this second type of heat transfer that is of particular interest in this paper.

A word should be inserted here regarding units. Non-advective processes are generally measured in heat per unit surface area per unit time. Advective processes are generally computed in heat per system per unit time. The conversion factor is the average surface area of the lake, and it is up to the individual investigator to select the units that are best suited to his individual problem.

A lake is an *open* thermodynamic system, inasmuch as there is an exchange of mass with its surroundings, and the total mass of the system may vary with time. It is thus necessary to

1. establish the continuity of mass of the system, and

2. establish the heat transfer for all components of mass transfer.

The equation of continuity of the lake can be stated simply that the change in mass of the lake during a given period must equal the net advection into the lake. If we neglect changes in density, such as that due to thermal expansion, the continuity equation can be written in terms of volume.

$$V_2 - V_1 = V_I - V_O + V_G + V_P + V_R - V_K - V_e \qquad (2)$$

where

V_2 = volume in lake at end of period
V_1 = volume in lake at beginning of period
V_I = volume inflow from rivers
V_O = volume outflow at dam or by outflowing rivers
V_G = volume gain by seepage
V_P = volume gain by precipitation
V_R = volume gain by surface run-off
V_K = volume loss to bank storage
V_e = volume loss by evaporation.

The lake volumes on the left hand side of Equation 2 are associated with the change in heat storage of the heat budget equation. All of the terms on the right hand side except the last are associated with the heat advection term of the heat budget equation, and the last is associated with the evaporation term. Because the purpose is to solve for evaporation using the heat budget, all other volumes of Equation 2 must be accounted for in some manner when computing the storage and the advection terms of the heat budget.

Note here, that if all of these volumes were known to sufficient accuracy the evaporation could be determined directly using Equation 2. This is rarely the case, however, having been accomplished to our knowledge only in the Lake Hefner studies. The advantage in accuracy obtained by using the heat budget over that obtained using the water budget can best be seen later after first developing the relationship between the water budget and certain terms in the heat budget.

A measure of the "total heat" per unit mass of water is accomplished by designating the amount of heat q_w necessary to bring it to the given temperature T from some base temperature T_B.

$$q_w \equiv \int_{T_B}^{T} c\, dT = c(T - T_B) \tag{3}$$

where c is the specific heat. (Note: Since specific heats at constant volume and at constant pressure are practically equal for water, both equations for enthalpy and for internal energy used in meteorology reduce to the above form.) Thus, the heat associated with any given volume is determined by numerically integrating equation (3) over the total mass. For example, since density, ρ, can be considered constant, the heat associated with the inflow is

$$Q_I = \rho \int_{V_I} q_I\, dV = \rho c \sum_{i=1}^{n} (T_{Ii} - T_B)\Delta V_{Ii} \tag{4}$$

When working with periods of one week to one month, since the temperature usually changes very little, this can be calculated by

$$Q_I = \rho c(\overline{T}_I - T_B)V_I \tag{5}$$

$\overline{T}_I$ is the *weighted mean temperature* if the equation is to hold strictly, but the *mean temperature* is generally satisfactory within the accuracy of the problem.

In the case of the change in heat storage one is interested in the difference in heat in the lake between the first of the period and the end of the period. Since the temperature varies with depth in the lake, one numerically integrates using increments of volume for each layer in which the temperature is constant or in which an average temperature can be used.

$$Q_\vartheta = \rho c \sum_{i=1}^{n} (T_{2i} - T_B)\Delta V_{2i} - \rho c \sum_{i=1}^{m} (T_{1i} - T_B)\Delta V_{1i} \tag{6}$$

where the subscript 2 refers to conditions at the end of the period and 1 to the beginning of the period. Note that the volume of the lake is not necessarily the same at the beginning and end of the period, nor need the same layers necessarily be used in each summation.

Such quantities as Q_I, Q_ϑ, etc., are seen to depend upon the total volume summed. Therefore, a physical interpretation or comparison with another quantity of unequal volume or a radiation term is not valid. All heat terms in which the water budget enters must be considered as a group. This includes the change in heat storage, the advected heat, and, as will be seen, a portion of the evaporation term.

For water vapor in equilibrium with the water surface at temperature T_e, the total heat per unit mass q_e contains the additional latent heat L_e at the temperature of evaporation.

$$q_e = L_e + c(T_e - T_B) \tag{7}$$

The heat loss associated with the mass evaporated is then

$$Q_e = \rho \sum_{i=1}^{n} L_{ei}\Delta V_{ei} + \rho c \sum_{i=1}^{n} (T_{ei} - T_B)\Delta V_{ei} \equiv Q_e' + Q_e'' \tag{8}$$

The evaporative heat loss comprises two parts denoted by the primed quantities on the right. Q_e' represents the heat loss by conversion of the water from the liquid to the vapor state at the temperature of evaporation T_e. Q_e'' accounts for the heat used to bring the water from the base temperature to the temperature of evaporation. *Q_e'' exists as a direct result of the mass continuity equation.* If one prefers, Q_e'' may be considered as a part of the mass advection, whereas Q_e' would be non-advective heat loss related to the latent heat of evaporation required for the change of state.

From the above equations we now have a modified form of Equation (1) which can be written

$$Q_\vartheta = Q_s - Q_b - Q_h - Q_e' - Q_e'' + Q_v \tag{9}$$

By introducing the weighted mean temperature of evaporation $\overline{T}_e$, the weighted mean latent heat of evaporation $\overline{L}_e$, and the Bowen ratio $R = Q_h/Q_e'$, Equations 8 and 9 give the evaporation

$$V_e = \frac{Q_s - Q_b + Q_v - Q_\vartheta}{\rho[\overline{L}_e(1 + R) + c(\overline{T}_e - T_B)]} \tag{10}$$

The use of arithmetic mean temperatures rather than weighted mean temperatures in Equation 10 will introduce errors that are small compared to possible errors in the evaluation of the observed and computed radiation terms. Units for V_e are in volume per lake per unit time or volume per unit area per unit time according to the working units originally selected.

The accuracy gained by using the heat budget can now be seen. In utilizing the water budget the evaporation is determined from the difference of large quantities, and *errors* in determining these quantities are the same order of magnitude as the evaporation. On the other hand the heat used in evaporating the small volume is of the same order of magnitude as the other quantities in the heat budget, because of the latent heat of evaporation.

The existence of the term $c(\overline{T}_e - T_B)$ in the denominator is the only variation from the heat budget evaporation equation given in early references. It is in the nature of a correction factor and, in general, does not alter greatly the computed evaporation. It prevents introduction of a constant bias into the computations, however. In the case of the Lake Hefner Water Loss Investigation where a base temperature of 0°C was used, an omission of this term would have resulted in computed evaporation from 2% to 5% too large.

The use of the base temperature which can be specified for the individual problem permits a flexibility in the use of the equation. In the first case, if there is a large error in the determination of some volume in the advection term its effect may be minimized. For example, seepage into or out of many lakes is known to exist, but the amount can be only crudely estimated. However, from the geological structure it may be determined in one case that the seepage is outward near the bottom of the lake and this temperature is known. The heat advected by this process, a part of Q_v, is

$$Q_G = \rho c \sum_{i=1}^{n} (T_{Gi} - T_B)\Delta V_{Gi} \qquad (11)$$

The closer the base temperature for the problem is set to the temperature of the seepage T_G, the nearer the heat advected by seepage term Q_G approaches zero, and the rough estimate of the seepage volume V_G is sufficient or not even necessary.

As a second case it is conceivable that by monitoring temperature of the inflow and making a good estimate of its weighted average temperature for use as the base temperature, fair values of evaporation could be obtained. This assumes, of course, that other major components of advection are measurable, the primary ones being the volume and temperature of outflow.

A third variation of the method would be to select the base temperature as the best estimate of the weighted average of more than one unknown volume, such as surface run-off and seepage. The individual thus has the latitude to select the method which gives the best result for his own particular problem.

SUMMARY

The heat budget can be used to obtain evaporation in the absence of precise measurements of the water budget, because the latent heat of evaporation appears in the denominator of the equation. The modified equation that is presented considers the mass continuity of the system and provides a flexibility in the use of the equation to minimize errors due to unknown quantities in the water budget.

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Epiphasic Carotenoids in Post-Glacial Lake Sediments

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ABSTRACT

The presence of α- and β-carotenes in surface mud from Lower Linsley Pond, Connecticut, and Little Round Lake, Ontario, was demonstrated by comparing the chromatographic positions and absorption spectra of the isolated compounds with authentic specimens of the same compounds prepared from carrots. Seven other carotenes were isolated from the Lower Linsley Pond mud, three of which were probably myxoxanthin, rhodoviolascin, and lycopene.

Carotenoids were found in sediment cores taken from Upper Linsley Pond and Bethany Bog, Connecticut. On the basis of radiocarbon dates and pollen zonations the age of the oldest sediments in these cores was estimated to be approximately 11,000 years. Carotenoids were present in the organic sediments at all depths, but were present in traces or not at all in the basal clay-silts. Five carotenoid zones of the paper chromatograms were estimated separately using an arbitrary concentration scale: carotene (consisting of α- and β-carotenes and perhaps their *cis*-isomers as well), myxoxanthin (?), rhodoviolascin (?), and two unidentified epiphasic carotenoids termed compounds A and B. In the core from Bethany Bog, rhodoviolascin was maximal in the upper part, carotene in the middle, and myxoxanthin and compound B in the middle and lower parts. Myxoxanthin, a pigment of the blue-green algae, was present only in sediments of the mesotrophic phase of the history of Bethany Bog, and not in those of the dystrophic (bog) phase. The same pigments obtained from the Bethany Bog core were found in a core from Upper Linsley Pond, but the changes in concentration with depth were less striking. A new yellow pigment was present in the Upper Linsley Pond samples.

Data on the biochemical composition of mud may be important in determining the kind and amounts of plant tissues incorporated into the mud.

INTRODUCTION

During the past thirty years a few isolated papers have been published dealing with the preservation of organic compounds in fossils and sedimentary deposits. Abelson (1954) has introduced the term paleobiochemistry to cover investigations of this sort, and has laid a firm foundation for the subject by demonstrating that amino acids are present in fossil shells and bones as old as the Devonian period. The paleobiochemistry of the post-Pliocene has been reviewed by Vallentyne (1956) and that of the pre-Pleistocene is currently under review (Vallentyne, in preparation). No more need be said here other than to indicate that the data of paleobiochemistry have important bearing on such problems as biochemical evolution, paleontology, geothermal gradients, and perhaps even the origin of life. The present paper lies within the scope of this framework as it applies to the study of lake history, and in particular to the preservation of carotenoids in lake sediments.

The carotenoids comprise a group of about 80 colored lipoidal substances which have the following properties in common: the presence of 40 carbon atoms per molecule; a system of ethylenic bonds, most of which are conjugated; and well defined light absorption maxima from 400 to 600 mμ. The carotenoids are divisible into two groups on the basis of phase distribution between 90% methanol and petroleum ether: the carotenes (epiphasic) which are hydrocarbon in nature and pass to the upper petroleum ether phase, and the xanthophylls (hypophasic) which pass to the lower methanol phase. The structural basis for the distinction is the number of hydroxyl groups per molecule. The carotenes possess none and the xanthophylls two. A few caroten-

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oids have one hydroxyl group molecule. These can be distinguished by their partly epiphasic behaviour with 90% methanol, but hypophasic behaviour with 95% methanol. The xanthophylls frequently occur in nature as esters of organic acids. Saponification is necessary before the xanthophyll component can be isolated in pure form. The chemistry of carotenoids has recently been summarized by Karrer and Jucker (1950) and the biochemistry by Goodwin (1952).

I should say first of all that the preservation of carotenoids in sediments comes as a surprise to those who are not familiar with the fact that wet sediments are devoid of oxygen (except perhaps for the uppermost few cm), for the carotenoids are quite sensitive to oxidation by air. The oxidation is catalyzed by light and high temperatures, but again these factors are unlikely to operate in a wet sediment. The sediment is therefore an admirable medium for the preservation of such compounds.

Trask and Wu (1930) were the first to report the presence of carotenoids in surface sediments. Later and more extensive work was carried out by Baudisch and von Euler (1934), Klimov and Kazakov (1937), Fox (1937), Muraveisky and Chertok (1938), Lederer (1938), Karrer and Koenig (1940), Beatty (1941), Fox and Anderson (1941), Fox, Updegraff, and Novelli (1944), Phinney (1946), Savinov, Mikhailovnina and Shapiro (1950), Andersen and Gundersen (1955) and Züllig (1955, 1956). About twenty different carotenoids have been found in sediment extracts; however only two of these have been identified with absolute certainty: β-carotene (Savinov, Mikhailovnina, and Shapiro 1950) and rhodoviolascin (Karrer and Koenig 1940). Only in these cases have the properties of the sedimentary compounds been directly compared to those of the authentic compounds. The oldest deposit from which carotenoids have been isolated is an interglacial gyttja studied by Andersen and Gundersen (1955), which was estimated to be 100,000 years old.

From the little that is known, there is no difference between marine and freshwater sedimentary carotenoids other than that expected from the different types of plant and animal remains that become incorporated in the sediments. There may be a slight predominance of carotenes over xanthophylls in sediments (Fox, Updegraff, and Novelli 1944), although exceptions are known (Muraveisky and Chertok 1938). Fox, Crane, and McConnaughey (1948) have noted that most marine animals tend to reject carotenes and absorb the xanthophylls supplied as food. Apparently the most important factor in the breakdown of carotenoids in wet *sediments* is attack by microorganisms (Fox 1948, Fox and Oppenheimer 1954). So far as I am aware, carotenoids have not been recovered from lithified sediments. Whether this is due to their absence or the lack of critical investigation is a point worthy of future investigation.

The present work was undertaken as an attempt to identify some of the carotenoids of Connecticut lake sediments and to learn if quantitative data on the distribution of these compounds in lake sediment cores might have bearing on the history of vegetation in the lakes studied. It is well to recall that virtually all approaches to the study of post-glacial vegetation are based on morphology. Visual recognition becomes impossible when form is not preserved, and in such cases a biochemical method could be a useful substitute. The biochemical approach is subject to just as much, if not more, uncertainty in interpretation, but since the preservation of form and chemical composition are subject to different laws, the two methods may find harmonious use in conjunction with each other.

The early progress of this work was aided by a grant from the National Science Foundation to Professor G. Evelyn Hutchinson. Later work was supported by the National Research Council of Canada and the Research Council of Ontario. For help, encouragement, and advice, I am indebted to G. Evelyn Hutchinson, E. S. Deevey, D. A. Livingstone, and H. Ignatius. Most of the data presented here were used for a thesis submitted to the Graduate School of Yale University in partial fulfillment of the

requirements for the degree of Doctor of Philosophy. A preliminary report of the major results has been published (Vallentyne 1954).

LOWER LINSLEY POND, CONNECTICUT

References to the biology and chemistry of this eutrophic lake are listed by Vallentyne and Swabey (1955).

For the qualitative analysis of epiphasic carotenoids an Ekman dredge sample of mud (4.4 kg wet weight) was collected at 12 m depth. The sample was extracted at room temperature in an atmosphere of nitrogen, first with methanol (20 L), then with petroleum ether (15 L) until the extracts were nearly colorless. The methanol extract was driven into petroleum ether by dilution with water. The combined petroleum ether extracts were then evaporated *in vacuo* to about 300 ml and saponified (with shaking) with an equal volume of 20 % methanolic KOH (20 hours at room temperature under an atmosphere of nitrogen). The base and methanol were removed by dilution and repeated washings with distilled water. The petroleum ether phase was shaken with an equal volume of 90 % methanol to remove the small amount of xanthophylls freed by saponification. The methanol was removed by repeated washing with water and the petroleum ether phase dried with anhydrous Na_2SO_4. The petroleum ether extract was then concentrated to about 2 ml and chromatographed on a column of alumina (175 x 25 mm) using petroleum ether (B.P. 30–62°) as the developer. Development was continued until the most loosely adsorbed zone had passed through the column. The colored zones were then cut out, eluted with benzene containing 3 % methanol, and rechromatographed on MgO or (in the case of the α- and β-carotene fractions) on $Ca(OH)_2$. The appearance of the chromatograms is shown in Figure 1. Elution from the final columns yielded relatively pure carotenoids. Each fraction produced a bluish color with $SbCl_3$ in chloroform (the Carr-Price reaction) indicating the carotenoid nature of the pigments. Phase distribution showed that each fraction was epiphasic to both 90 and 95 % methanol. A Beckman Model DU spectrophotometer was used to determine the spectra of the different fractions. Pertinent data regarding each fraction are listed in Table 1. The colors listed in the table refer to those on the final columns, not in solution.

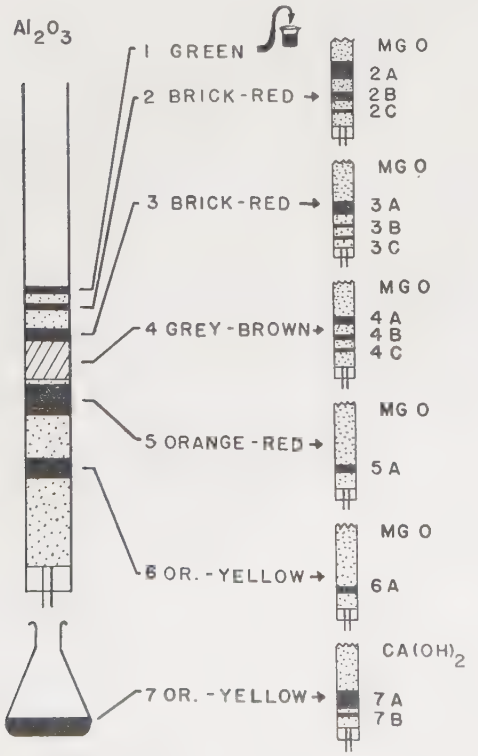

FIG. 1. Separation scheme for epiphasic carotenoids in an extract of Lower Linsley Pond mud. 1, sedimentary chlorophyll degradation products; 2A, unidentified; 2B, unidentified; 2C, rhodoviolascin; 3A = 4A, compound A; 3B = 4B, unidentified; 3C = 4C = 5A, myxoxanthin; 6A, lycopene; 7A, β-carotene; 7B, α-carotene.

Identification of the carotenoids was based on relative chromatographic position, absorption maxima, and phase distribution. Insofar as the isolated compounds were not directly compared with authentic carotenoids, the identifications are only tentative. However subsequent work has made it clear the identifications of α- and β-carotenes were correct. The identities of 2c, 5a, and 6a as rhodoviolascin, myxoxanthin, and lycopene, respectively, are less certain. One can only say that the properties of the isolated compounds do not disagree with the tentative identifications.

TABLE 1. *Carotenoid fractions from column chromatography of an extract from Lower Linsley Pond mud*

An asterisk (*) indicates too low a concentration for a reliable determination of the absorption maxima.

Fraction	Color	Abs. max. in CS_2 mμ	Remarks
1	green	—	sedimentary chlorophyll degradation products
2a	very faint pink	*	unidentified
2b	faint yellow	*	unidentified
2c	orange-red	570, 527, 499	rhodoviolascin ? (abs. max., 473, 534, 496). Could be torulene.
3a	yellow	509, 482, 451	compound A; properties do not agree with any known carotenoid
3b	very faint pink	*	unidentified
3c	orange-yellow	single band, 488–496	myxoxanthin ? (abs. max., single band at 488).
4a	yellow	510, 482, 451	= 3a
4b	faint pink	*	= 3b
4c	orange-yellow	single band, 488–494	= 3c, myxoxanthin ?
5a	orange-yellow	single band, 488–496	= 3c = 4c, myxoxanthin ?
6a	orange-yellow	547, 510, 483	lycopene ? (abs. max., 548, 507, 477).
7a	orange	518, 489, (452)	β-carotene (abs. max., 520, 485, 450).
7b	yellow	510, 479, (452)	α-carotene (abs. max., 509, 477). The shoulder at 452 may indicate contamination with β-carotene.

The occurrence of α-carotene, β-carotene, and lycopene in the sediment of this (or any) lake is to be expected because of the wide distribution of these compounds in the plant kingdom. Myxoxanthin (= echinenone) is a carotenoid which (among freshwater organisms) is found only in the blue-green algae. Its occurrence in the mud of Linsley Pond was not unexpected, for blue-green algal blooms are common in that lake during the summer. It was surprising, however, that a microscopic examination of surface sediment from the lake failed to reveal the presence of any blue-green algal cells. The fact that these algae are present in the plankton necessitates that their partly decomposed bodies sink and enter into the composition of the mud. Since they are not morphologically recognizable there, it is clear that the pigment myxoxanthin must be more stable in the mud than the structure of the cell wall. The morphology of fossil blue-green algae is preserved in some lakes (Lundqvist 1927), but this is apparently not the case in Linsley Pond. The above argument is of course valid only if the identification of myxoxanthin is correct. Subsequent work has indicated that the identification was probably not in error. Fractions with chromatographic and spectral properties similar to the myxoxanthin (?) from Lower Linsley Pond mud have since been isolated from mud and a sample of seston rich in *Anabaena*, both from Lake Opinicon, Ontario.

Rhodoviolascin is a pigment best known from the purple bacteria (Karrer and Jucker 1950). Although purple bacteria have not been isolated from the mud of Linsley Pond, their presence is to be expected. The identity of the rhodoviolascin (?) isolated is less certain than that of myxoxanthin.

The pigments isolated from Lower Linsley Pond mud by column chromatography were chromatographed separately and together on paper, using petroleum ether as the developer. The positions of each of the fractions on paper chromatograms are shown in Figure 2. One unidentified pigment, which

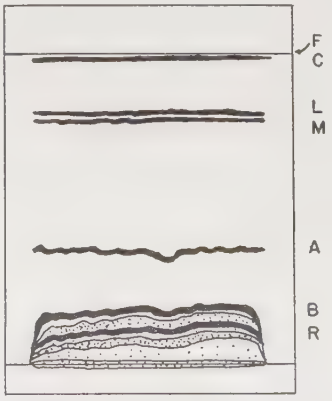

FIG. 2. The characteristic appearance on a paper chromatogram of an acetone extract of a core sample. Epiphasic carotenoid zones shown in black (C = carotene, L = lycopene, M = myxoxanthin, A = compound A, B = compound B, R = rhodoviolascin). Sedimentary chlorophyll degradation products shown as stippled zones. Positions of xanthophylls not shown. F = solvent front.

I shall call compound B, was present on paper chromatograms of core samples but was not present in the surface mud sample from Lower Linsley Pond. The chromatographic position of compound B is shown in Figure 2 together with the positions of the sedimentary chlorophyll degradation products (SCDP) which were present on chromatograms of core extracts. The latter two groups of pigments were not measured quantitatively because of the overlapping of the zones.

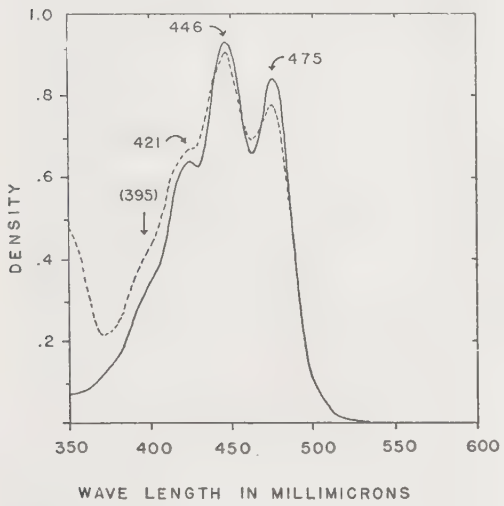

FIG. 3. Absorption spectra of α-carotene from carrots (solid line) and α-carotene from the mud of Little Round Lake, Ontario (dotted line). Solutions adjusted to approximately equal density. Solvent: *n*-hexane.

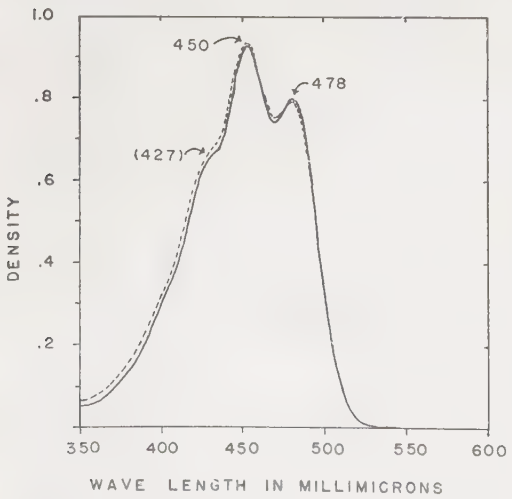

FIG. 4. Absorption spectra of β-carotene from carrots (solid line) and β-carotene from the mud of Little Round Lake (dotted line). Solutions adjusted to approximately equal density. Solvent: *n*-hexane.

Note from Figure 2 that α- and β-carotenes cannot be separated on paper. Subsequent test has further shown that the *cis*-isomers of these compounds occupy the same position on paper chromatograms as the all-*trans* compounds. Lycopene and myxoxanthin are poorly separated at best; however an absorption spectrum clearly shows the difference. Lycopene has three separate absorption peaks, myxoxanthin only one.

LITTLE ROUND LAKE, ONTARIO

This is a small lake, about 10 acres in area, located in eastern Ontario on the north side of Highway No. 7, one-half a mile west of the junction of Highways No. 7 and No. 38. The lake has a maximum depth of 16 m. The phytoplankton population is always low, indicating that the lake is probably unproductive. On the other hand, the mud is about 50% organic and contains the highest amounts of carotenoids and SCDP of any sediment that we have ever examined.

An Ekman dredge sample of mud (about 0.5 kg wet weight) from a depth of 16 m was used for the purpose of isolating α- and β-carotenes. The wet mud was extracted with acetone (3 L) and the acetone extracts transferred to petroleum ether by dilution with water. After saponification and concentration of the petroleum ether extract by vacuum distillation, the pigments were chromatographed on a column of $Ca(OH)_2$ (150 x 25 mm) using petroleum ether (B.P. 30–62°) as the developer. The zones corresponding to α- and β-carotenes were eluted and each separately chromatographed in the same way three times further. In a like manner pure α- and β-carotenes were prepared from carrot roots. Figure 3 shows the visible light spectra for α-carotene from the two sources, and Figure 4 for β-carotene from the two sources. The α-carotene from the mud was contaminated with ultraviolet light absorbing impurities, but otherwise the visible spectrum showed a fairly close resemblance to the same compound derived from carrots. In the case of

β-carotene, the superposability of the two spectra leaves little doubt as to the identity of the mud compound. Finally, the samples of α-carotene from the two sources, when mixed in equal quantities, were found to be chromatographically inseparable on columns of $Ca(OH)_2$ developed with petroleum ether. The same was true of the samples of β-carotene from the two sources. The similarity of the spectra and the evidence from mixed chromatograms corroborate the tentative identifications.

BETHANY BOG, CONNECTICUT

The possibility that carotenoids might persist in old Connecticut lake muds was too inviting to remain untested. The first sediment core was taken from Bethany Bog (located about 10 miles NW of New Haven, Connecticut). The lake has been almost completely obliterated by the development of a bog mat, leaving only a few square meters of open water. The accumulated sediments of the lake have been analyzed for pollen by Deevey (1943) and for diatoms by Patrick (1954). The diatom determinations were made from samples of the core described below.

The boring was made at the edge of the bog mat surrounding the open water with the aid of Davis and Hiller borers. Samples were collected at 1 m depth intervals. The Davis borer was used for the first 6 m and the Hiller borer for all deeper samples. Penetration of the sediment beyond a depth of 14.7 m proved impossible. A sample at a depth of 1 m could not be collected due to the watery nature of the material there. Two other samples, at 9.5 and 10.5 m, were collected at the same site with a Davis borer two months after the original collection. All samples were preserved in glass jars in a dark room at 4°C between the time of collection and analysis (two months between collection and completion of analysis). Preservative was not added to the samples at any time. There was no evidence of a change in the carotenoids under these storage conditions.

The sequence of sediments deposited by the lake was as follows. The samples at 14.7 and 14 m were composed of clay-silt. The 13 m sample was a clay gyttja. Samples from 12–9 m inclusive were of the algal gyttja type, while those at 8 m and above were dy. From an examination of the diatoms preserved in these samples Patrick (1954) concluded that the sediments at 14.7 and 14 m were deposited by a lake that was oligotrophic at the time of deposition. The diatoms present in the 13–9 m samples suggested the conversion to, and development of, a mesotrophic lake. A transitional flora in the 8 and 7 m samples pointed to the beginning of bog conditions, while the samples at 6 m and above were characteristic of a dystrophic (bog) lake. Such is the sediment sequence as it reflects the history of the lake.

Before extraction, the samples were dried in a nitrogen-filled desiccator until constant weight was obtained. Samples (1–2 g dry weight) were ground in a mortar and then completely extracted with 95% acetone (400–800 ml). The acetone extracts were evaporated to dryness by vacuum distillation. No special precautions were taken to exclude oxygen, except that the passage of air through the vacuum apparatus was reduced to a minimum. Later tests showed that about 20% of the carotenoids were destroyed during this process, as compared to control vacuum distillations under nitrogen. The losses were found to be constant for different samples. The distillation residue was dissolved in 10 ml of absolute acetone, and fractions (1 to 4 ml depending on the concentration of the pigments) were streaked on base lines drawn on two sheets of Whatman № 1 filter paper (previously dried in an oven at 80°C). The papers were stapled into the form of cylinders and the chromatograms developed in the ascending manner in an atmosphere of nitrogen (Bauer 1952). Petroleum ether (B.P. 30–62°C) was used as the developer, and the process was complete in about 8 hours. The appearance of the chromatograms was roughly as shown in Figure 2. Occasionally there were yellow zones just below the carotene zone. These were not systematically analyzed. No attempt was made to estimate the xanthophylls since they were overlapped by the green chlorophyll-like material. The entire process of extraction and chromatography was carried out under

darkened conditions in order to minimize the amount of carotenoid breakdown.

Paper chromatography of carotenoids, as performed in this way, is not an effective method of separation. There are however, two advantages over columns that give the paper method superiority: the speed and reproducibility of the process, and the ease of recovery of the carotenoids.

The colored zones on the paper chromatograms were known to be mixtures in one case (the carotene zone), and in two other cases the identity of the carotenoid was unknown (compounds A and B). Identification of the other epiphasic carotenoids (myxoxanthin and rhodoviolascin) are only tentative. Under such circumstances the quantitative data cannot be reported in terms of weight of carotenoids per unit weight of mud. A relative scale had to be adopted. The procedure was to cut the colored zones into small pieces which were placed in the bottom of a test tube. A known volume (5–15 ml) of peroxide-free diethyl ether was added and mixed with the paper until all the color had been eluted. The absorption spectrum was then determined with a Beckman Model DU spectrophotometer, making particularly careful readings at the positions of absorption maxima. Concentrations are reported in terms of an arbitrary scale of pigment units. The method of calculation is outlined below.

The acetone extract of 1.247 g dry weight of mud was evaporated to dryness and redissolved in 10 ml of absolute acetone. Aliquots (4 ml) were streaked along base lines drawn on two sheets of Whatman № 1 filter paper. The colored zones were cut out after the development of the chromatograms. The carotene zones (for example) were eluted, each with 5 ml of diethyl ether. Density readings at the main absorption maximum were 0.175 and 0.180 (average, 0.177).

$$\text{Carotene} = \frac{\text{Av. density reading at abs. max.}}{\text{Dry wt. extracted in g}} \times \frac{\text{Vol. of ether}}{\text{Fraction of acetone put on chromatogram}}$$

$$= \frac{0.177}{1.247} \times \frac{5}{0.4}$$

$$= 1.77 \text{ pigment units per g}$$

Quantities of the other pigments were determined in the same way. It will be apparent that the relative scale of pigment units for one chromatographic zone applies only to that zone, for extinction coefficients vary with the carotenoid. For any single chromatographic zone that is a mixture of more than one carotenoid, the relative scale is valid providing there is not too much change in the composition of the mixture.

The overall reproducibility of the method was tested by running five separate analyses on a homogeneous mud sample. No result deviated more than 20% from the average and most were within 10%. The method is therefore semi-quantitative. For carotene, compound B, and rhodoviolascin the wave lengths at which absorption was maximal (using diethyl ether as the solvent) were 450, 450, and 528 mμ, respectively. The nitrogen content (NH_3-N plus organic-N) of the sediment samples was determined using the method of Boell and Shen (1954) modified for use in the micro range. Ignition loss was determined by ashing over a Bunsen burner.

Data for carotenoids in the Bethany Bog core are recorded in Table 2 together with other pertinent information. The data for SCDP are taken from Vallentyne (1955). The most interesting feature of Table 2 is the change in carotenoid concentrations with depth. The carotene fraction was the most prominent of the epiphasic fractions. Carotene was present in the greatest concentration not at the surface, but at a depth of 9–9.5 m. Rhodoviolascin on the other hand was concentrated in the uppermost (peaty) part of the profile, although it was lacking in the sample of surface vegetation, as would be expected. Compound B was present in highest amounts in the gyttja and was barely detectable in the peat. The cause of the relatively high concentration of SCDP at 12 m is not known. The important point is that not all the carotenoid fractions decrease in concentration as the depth (and hence the age) increases. Two other chromatographic zones (compound A and myxoxanthin) were present in amounts so small that only their presence or absence could be noted. Little can be said of com-

TABLE 2. *Chemical analysis of a sediment profile from Bethany Bog, Connecticut*

See text for explanation of the term "pigment units". Nitrogen is the sum of NH_3-N and org.-N. The data for sedimentary chlorophyll degradation products (SCDP) are from Vallentyne (1955). Lake types according to Patrick (1954). Abbreviations: oligotrophic (o), mesotrophic (m), dystrophic (d), not determined (nd).

Depth (m)	Lake type	Ignition loss (%)	Nitrogen (%)	Pigment units per g dry weight					
				Carotene	Compound B	Rhodoviolascin	Compound A	Myxoxanthin	SCDP
0	d	94.5	1.6	1.8	+	0.0	−	−	28.1
2	d	76.7	2.7	4.2	+	4.5	+	−	40.1
3	d	74.0	2.1	2.1	0.5	2.0	−	−	39.8
4	d	65.7	2.2	5.0	+	3.0	+	−	48.8
5	d	62.2	2.3	4.5	+	3.0	+	−	52.5
6	d	65.4	2.4	2.8	+	1.4	+	−	39.3
7	m-d	61.8	2.3	4.6	0.5	1.0	+	+	39.5
8	m-d	58.6	2.3	8.4	1.4	0.9	+	+	42.5
9	m	47.1	1.6	12.4	0.9	0.6	+	+	35.9
9.5	m	nd	1.6	12.7	2.1	nd	nd	nd	nd
10	m	35.0	1.5	5.0	0.8	0.4	+	+	27.5
10.5	m	nd	1.5	4.1	0.8	0.4	nd	nd	nd
11	m	36.7	1.7	8.7	1.3	0.8	+	+	24.9
12	m	49.1	1.3	6.9	2.6	1.3	+	+	57.6
13	o-m	29.2	0.2	0.4	0.1	0.0	−	−	—
14	o	3.4	nd	0.0	0.0	0.0	−	−	0.0
14.7	o	5.4	nd	0.0	0.0	0.0	−	−	0.0

pound A since its identity is unknown, but the pattern for myxoxanthin is striking: it was found only in the sediment deposited during the mesotrophic phase of the lake's history, and not in the peat. Thus when the diatom evidence (Patrick 1954) shows a change from mesotrophy to dystrophy, the myxoxanthin becomes undetectable in the sediment. This probably indicates a relative decrease in the abundance of blue-green algae coupled with the onset of dystrophy. In modern lakes extensive blooms of blue-green algae are certainly less common in humic waters than in unstained waters. The carotenoid history of Bethany Bog shows the transition in time.

Is it possible that some of the carotenoids in this core were synthesized after deposition of the sediment? While a definite answer cannot be given, it is probable that some post-depositional synthesis did occur. Snow and Fred (1926) succeeded in culturing colored bacteria from lake sediments, and it seems reasonable that the bacterial pigments were partly carotenoid in nature. I am inclined to think that the amount of post-depositional synthesis of carotenoids would be small in comparison to the direct source of carotenoids from the sinking bodies of dead phytoplankters. In any case, post-depositional synthesis is probably limited to the uppermost meter of sediment, for the decline in culturable bacteria with depth is logarithmic (Henrici and McCoy 1938). The pattern of myxoxanthin occurrence and the high amounts of carotene in the late mesotrophic stage of the lake's history suggest that the amounts of these carotenoids preserved in the mud are proportional to the amounts originally deposited. This interpretation is strengthened when the carotenoid data are plotted (as shown in Figure 5) in terms of pigment units per g of ignitable matter, a method that shows marked enrichment of carotenoids in the organic matter of the gyttja as compared to the peat.

The above data, if correctly interpreted, suggest that carotenoids may validly be used

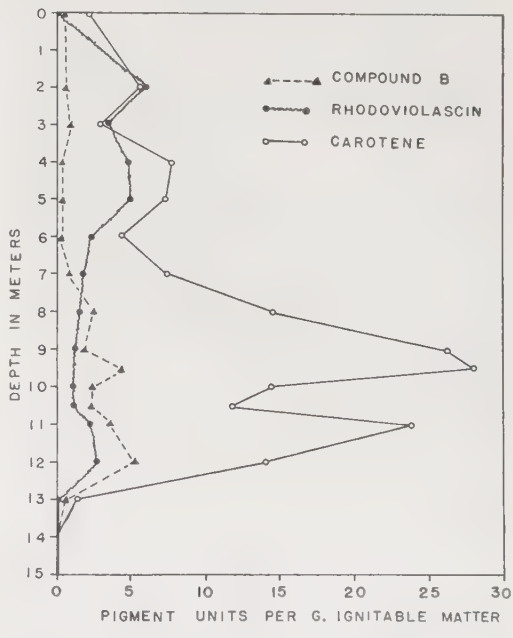

FIG. 5. Compound B, rhodoviolascin, and carotene in a sediment core from Bethany Bog, Connecticut. Concentrations expressed as pigment units per gram ignitable matter. The values for the 9.5 and 10.5 m samples are included on the assumption that the ratios of ignition loss to N are constant from 9–11 m.

as biochemical fossils. In connection with the study of Bethany Bog it is interesting to note that Vallentyne and Bidwell (1956) found free glucose in the gyttja section of the Bethany Bog core. Although the amounts were exceedingly small, there was a definite rise to a maximum at the same level where carotene was maximal (9 m). The meaning of the sugar data is not clear (see Vallentyne and Bidwell 1956) but the carotenoid data do lend positive support to Patrick's (1954) conclusion that the lake was most productive when the 11–9 m sediments were deposited.

UPPER LINSLEY POND, CONNECTICUT

Upper Linsley Pond is a shallower and less productive lake than the lower pond which lies just across the road. The lake has a maximum depth of 6 m. The upper pond is surrounded by a bog mat but otherwise shows only incipient signs of dystrophy. The sediments of Upper Linsley Pond have been analyzed for pollen by Deevey (1943). Two profiles of the sediment have been radiocarbon-dated (See Flint and Deevey 1951 for a discussion of the radiocarbon dates).

The samples analyzed in the present study were collected with a Davis borer from the deepest part of the lake. In order to prevent the borer from opening while being lowered through the water, the cylinder and piston were held together with scotch tape. The tape was easily broken on taking the samples. Samples were collected at irregular intervals down to a depth of 13 m, *i.e.*, through 7 m depth of sediment. Penetration below 13 m proved impossible due to bending of the connecting rods in the water. The 13 m sample was composed of clay-silt with very little organic matter. Samples from all higher levels were of the gyttja type, diluted with clay in the deeper part of the core.

Treatment of the samples and measurement of carotenoid concentrations were identical to those described for the Bethany Bog core, with two exceptions:

1. The vacuum distillation of acetone extracts of the dried mud was carried out in an atmosphere of coal gas. This was done to introduce a reducing atmosphere, thus lessening the possibility of oxidative breakdown during concentration. Although nitrogen would have been preferable, a supply was not on hand when the analyses were started.

2. The epiphasic carotenoid zones were eluted from paper chromatograms with CS_2 instead of diethyl ether. The use of CS_2 is preferable because the absorption maxima of the carotenoid zones can then be directly compared with the table of CS_2 maxima in Karrer and Jucker (1950). The wave length of maximal absorption for both carotene and compound B in CS_2 was 480 mμ.

The pollen counts were made by H. Ignatius. The pollen stratigraphy of the core was essentially the same as that previously described by Deevey (1943). From the pollen stratigraphy and the radiocarbon dates listed by Flint and Deevey (1951) for samples from the middle of the lake, it is estimated that the 13 m sample was deposited roughly 11,000 years ago. The age of the *B–C1* boundary is 8,300 years and that of the *C1–C2* boundary 5,200 years (Flint and Deevey 1951).

Data obtained by chemical analysis of the Upper Linsley Pond samples are presented in Table 3 together with other pertinent data.

TABLE 3. *Chemical analysis of a sediment profile from Upper Linsley Pond, Connecticut*

Pollen zone nomenclature according to Deevey (1943). For explanation of other terms see Table 2. Depth refers to that below the water surface. Mud-water interface at a depth of 6.0 m.

Depth (m)	Pollen zone	Ignition loss (%)	Nitrogen (%)	Pigment units per g dry weight				
				Carotene	Compound B	Compound A	Myxoxanthin	SCDP
6.5	C3	69.6	3.3	4.9	1.4	+	+	nd
7.2	C2	62.3	2.2	3.3	1.2	−	+	41.2
7.9	C2	61.8	2.8	2.1	0.6	−	−	48.1
8.7	C1–C2	60.4	2.7	1.1	0.6	−	−	36.2
9.4	C1	59.1	2.1	5.3	0.9	+	+	33.7
10.3	C1	60.0	2.2	2.1	0.2	−	−	37.6
11.0	B–C1	59.8	2.4	3.9	1.2	+	+	39.7
11.7	A	20.0	0.8	1.9	1.0	+	+	15.5
12.2	A	26.0	1.2	2.0	0.8	+	+	20.0
13.0	A	3.7	0.1	0.9	0.1	+	+	0.8

The data for SCDP are taken from Vallentyne (1955), and the pollen zonations are based on Deevey's (1943) nomenclature. The pattern of colored zones on the chromatograms was similar to that previously encountered in the Bethany Bog study, except that the position of rhodoviolascin was overlapped by a new yellow carotenoid. For this reason the rhodoviolascin zone was not measured quantitatively. The highest amounts of rhodoviolascin (as evidenced by color on the chromatograms) were present in the 11.7 and 11.0 m samples. It can be seen from Table 4 that although the percentage ignitable matter was constant from 11.0 to 7.2 m, the carotene content varied considerably from level to level, perhaps indicating changes in the type of organic material deposited. The most prominent feature was the low amount of pigment at the 8.7 m level. The silt-clay of the lowermost sample (unlike the silt-clay of Bethany Bog) contained some pigments. The amounts were small. The somewhat irregular pattern of changes in the concentration of myxoxanthin and compound A differs from the more "consistent" Bethany Bog pattern. The occurrence of myxoxanthin in at least some of the top, middle, and bottom levels of Upper Linsley Pond mud lends negative support to the suggestion that the absence of myxoxanthin in Bethany Bog peat was due to low populations of blue-green algae.

CONCLUDING REMARKS

This roughly fashioned study is but a preliminary attempt to investigate the occurrence and significance of carotenoids in sediments. The new results are:

(1) α- and β-carotenes from surface mud were found to be identical with the same compounds obtained from carrots.

(2) carotenoids were present in all organic samples (up to 11,000 years old) that were analyzed.

(3) it is suggested that the relative proportions of carotenoids that are preserved in fossil muds differ little from the proportions originally deposited.

The results obtained are in full accordance with those of other workers (Fox, Updegraff, and Novelli 1944; Andersen and Gundersen 1955) as regards the stability of carotenoids in sediments. What apears to be needed is a more critical qualitative study of the various carotenoids that are present in recent and old sediments. The present work was limited to epiphasic carotenoids because of limitations of time and ease of analysis. I am sure that a study of the hypophasic fractions would produce equally interesting data.

There is one problem that deserves special attention: the possible occurrence of *cis*-isomers of carotenoids in old sediments. Isomerization from the all-*trans* compounds would be expected to occur in deposits more than a few hundred years old. In fact, it is rather surprising that *cis*-isomers of β-carotene are not present in surface muds; however their absence from extracts of surface mud is shown not only by the present data but also by the work of others (Fox, Updegraff, and Novelli 1944; Savinov, Mikhailovnina, and Shapiro 1950). A 20,000 year old sample of mud from Searles Lake, California, is currently being examined for *cis*-isomers.

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Some Oceanographic Applications of Recent Determinations of the Solubility of Oxygen in Sea Water[1]

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ABSTRACT

The solubility of oxygen in fresh and sea water has recently been redetermined by Truesdale, Downing, and Lowden (1955), who found that the data of Fox (1909), long considered definitive, are in substantial error. The old and new data are compared, and the new are used to recompute the percentage saturation in the surface layer of the South Atlantic and equatorial North Atlantic Oceans from the METEOR observations. It is shown that most of the surface waters are in equilibrium with the atmosphere. The effects of the error on computations of oxygen consumption and of oxygen tension are discussed.

A new nomogram relating the equilibrium oxygen concentration, the temperature, and the salt content of the water is presented.

Truesdale, Downing, and Lowden (1955) have recently redetermined the solubility of oxygen in fresh and sea water, and have found that the data of C. J. J. Fox (1909), long considered definitive, are in substantial error.

Fox's data have been widely used in oceanography, limnology, estuary and sewerage studies to estimate the amount of oxygen in solution when equilibrium is established with a dry atmosphere at a total pressure of 760 mm of mercury. Whipple and Whipple (1911), recognizing that in nature the atmosphere at water surfaces is more apt to be saturated with water vapor than to be dry, published tables for the solubility of oxygen in fresh and sea water in equilibrium with moist air. They had begun their own determinations at the time Fox's data came into their hands, but since their figures were in substantial agreement with his they abandoned their experiments and based their tables on Fox's experimental work, thus lending authority to his data.

Truesdale, Downing, and Lowden (1955) were led to suspect that the accepted figures were in error by observations of rates of solution that departed from the Adeney and Becker (1919) law of aeration. They undertook new determinations after carefully establishing conditions which assured that the final solutions were in true equilibrium, neither under- nor super-saturated. They found solubilities appreciably smaller than Fox reported, and therefore presumed that both Fox and the Whipples were working with supersaturated solutions.

Kalle (1939) published a nomogram widely used in oceanography, based on Fox's dry air data, for making the computation of oxygen solubility. Other nomograms and tables have been published (e.g. Tully 1949), which relate the salt content, temperature, and oxygen solubility, based either on Fox's data or Whipple and Whipple's tables derived from them. We have prepared a nomogram, based on the new data, as a supplement to this paper (Fig. 1). It should be emphasized that the data are for equilibrium established under an atmosphere saturated with water vapor at the temperature in question. The solubility is expressed in parts per million (actually milligrams per liter: Truesdale, personal communication), and in milliliters at STP per liter. The scale for milligram atoms per liter printed on the nomogram may be cut off and substituted for either the ppm or ml/L scale if the user prefers this expression of concentration.[2]

A comparison of solubility values according to a) Fox's data, b) Whipple and

[1] Contribution No. 852 from the Woods Hole Oceanographic Institution.

[2] Copies of this nomogram, 13″ x 14″, are available on request from the Director, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

TABLE 1. *Comparison of values of O_2' (ml. O_2/liter) from Fox's (1909) dry air data (Col. 1), his data corrected for moist air according to Whipple and Whipple (1911) (Col. 2), and the new data for moist air of Truesdale, Downing, and Lowden (1955) (Col. 3)*

Temp. °C	S = 0 ‰			S = 20 ‰			S = 40 ‰		
	1	2	3	1	2	3	1	2	3
0	10.29	10.29	9.92	9.02	9.00	8.74	7.71	7.69	7.56
5	9.03	8.95	8.65	7.95	7.87	7.65	8.86	6.80	6.64
10	8.02	7.92	7.65	7.10	7.01	6.78	6.17	6.09	5.94
15	7.22	7.10	6.84	6.42	6.33	6.08	5.62	5.53	5.35
20	6.57	6.43	6.18	5.87	5.73	5.52	5.17	5.03	4.87
25	6.04	5.85	5.67	5.40	5.23	5.07	4.74	4.59	4.47
30	5.57	5.32	5.27	4.90	4.77	4.70	4.33	4.17	4.13

Whipple's tables, and c) the new data of Truesdale *et al.* (Table 1), shows that the discrepancies are greatest in low-salinity, low-temperature water and least at high salinities and temperatures. In sea water having a salinity 35‰, the discrepancy between Fox's values corrected for moist air and the new values vary from 0.16 ml O_2/liter at 0°C. to 0.04 ml O_2/liter at 30°C. However, most oceanographers have computed oxygen solubility from Fox's dry air data, and these discrepancies vary from 0.18 ml O_2/liter at 0°C. to 0.33 ml O_2/liter at 30°C. The values in Table 1 were read from nomograms prepared by Kalle (1939) for Col. 1, A. C. Redfield (1948) for Col. 2, and that which accompanies the present paper for Col. 3.

APPLICATION OF OXYGEN SOLUBILITY DATA

In the following discussion, O_2 will be used to designate the actual oxygen content of a water sample. O_2' is the solubility of oxygen in water having the observed salinity and temperature when in equilibrium with a standard atmosphere of 760 mm of mercury. O_2'' is the solubility in water at the observed salinity and temperature when in equilibrium with an atmos-

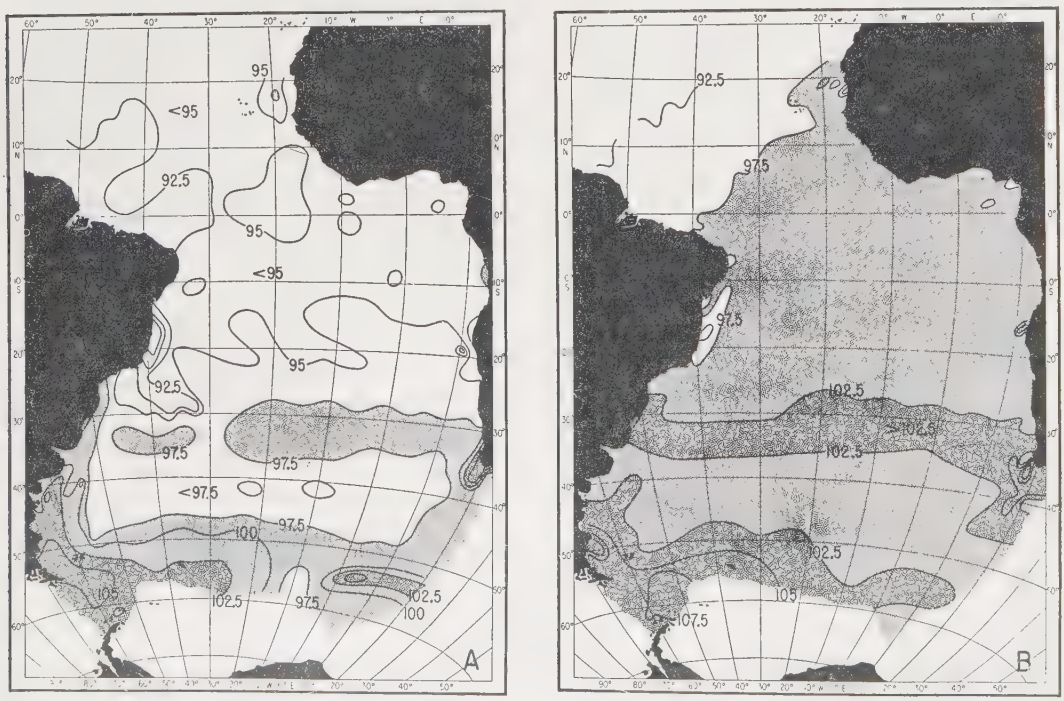

FIG. 2. Percentage saturation of oxygen in the surface layer of the equatorial North and South Atlantic Ocean. *A*. Redrawn from Wattenberg (1939), computed from the solubility data of Fox (1909). *B*. Recomputed from the METEOR data of Wüst (1932) and Wattenberg (1933, 1938), using the solubility data of Truesdale *et al.* (1955). The unshaded areas are less than 97.5% saturated, the lighter shading is in areas between 97.5 and 102.5% saturation, and the darker shading indicates greater than 102.5% saturation.

phere having the observed total barometric pressure and relative humidity.

In oceanography, values of O_2' have been used, *inter alia*, to compare with the observed oxygen concentration (O_2) in the computation of percentage saturation, *i.e.*, $\%\ \text{saturation} = \frac{O_2}{O_2'} \times 100$; the oxygen deficit (Brennecke 1909) or apparent oxygen utilization (Redfield 1942 *et seq.*), *i.e.*, $AOU = O_2' - O_2$; and the partial pressure or oxygen tension according to Henry's law, $p = P\frac{O_2}{O_2'}$, in which p is the partial pressure of oxygen in solution and P is the oxygen pressure in the atmosphere.

Wattenberg (1939, Beilage L) prepared a chart showing the percentage saturation of oxygen in the surface layer of the South Atlantic Ocean from the METEOR expedition data. This chart has been somewhat puzzling, showing, as it does, large areas of the surface to be 5 to 10% deficient in oxygen. In some regions one might expect the surface to be somewhat undersaturated, by virtue of the upwelling of undersaturated waters or by a high oxygen demand in the upper mixed layer in regions of high organic productivity. However, the distribution and the magnitude of the departures from 100% saturation shown by Wattenberg could not well be explained as results of these phenomena. Wattenberg's data have been recomputed and are shown, with a redrawing of his original chart for comparison in Figure 2. The most striking features of the revised chart are a) that in most of the South Atlantic Ocean the surface waters are essentially in equilibrium with the atmosphere, *i.e.*, 100% ± 2.5% saturated, b) that the surface is undersaturated in the region north of the equator, except in the eastern part, which is rich in phytoplankton and animal life (Hentschel 1936), and c) that the surface is supersaturated in the Subtropical Convergence, a region of high normal barometric pressures, and in the Antarctic Convergence, a region of large phytoplankton populations (Hentschel 1936). Conclusion a) is in marked contrast with Wattenberg's original findings, and the quantitative aspects of b) and c) are probably more accurately fixed by using the new oxygen solubility data.

Only some 10% of Wattenberg's computations were 100% ± 1%; the new data yield over 44% in this range. Appreciable undersaturation is still evident in the region north of the equator, and is apparently a manifestation of upwelling off the coast of Africa and of high oxygen demands resulting from high organic production farther to the west.

Significant supersaturation in the surface waters occurs across the ocean just north and south of 30° S. latitude and at the far-southern METEOR stations. These are regions of known convergence and/or of high phytoplankton growth and *in situ* production of dissolved oxygen. Other conditions, such as the warming of surface layers, departures of the total barometric pressure from normal (760 mm of mercury), and departures of the relative humidity from 100% (water saturated air) could result in values of the apparent percentage saturation departing from 100, even though equilibrium with the atmosphere exists. The METEOR data have been examined for these last two effects by computing the partial pressure of air in the atmosphere from the barometric pressure and relative humidity data of Kuhlbrodt and Reger (1938). These computations were made by application of the equation

$$O_2'' = O_2'\left[\frac{\left(P - p_t\frac{h}{100}\right)}{(760 - p_t)}\right]$$

O_2'' is the solubility of oxygen in water in equilibrium with an atmosphere having a total pressure of P mm of mercury and a relative humidity of h%.

O_2' is the solubility of oxygen in water in equilibrium with a water saturated atmosphere having a total pressure of 760 mm of mercury (the solubility data of Truesdale *et al.*).

p_t is the vapor pressure of water at t °C.

$(P - p_t\ h/100)$ is the partial pressure of air in the atmosphere.

These corrections make few qualitative changes in the data shown in Figure 2*B*: undersaturation and supersaturation are

TABLE 2. *Effect of total barometric pressure on apparent oxygen saturation from a water-saturated atmosphere at various temperatures*

Barometric pressure, mm of mercury	Apparent per cent saturation		
	0°C	20°C	35°C
720	94.68	94.48	94.12
740	97.33	97.27	97.07
760	100.00	100.00	100.00
780	102.64	102.76	102.93

Apparent saturation is $\frac{O_2''}{O_2'} \times 100$, in which O_2'' is the oxygen solubility under the specified conditions, and O_2' is the oxygen solubility from a water-saturated atmosphere having a total pressure of 760 mm of mercury.

TABLE 3. *Effect of relative humidity on apparent oxygen saturation at various temperatures*

Total atmospheric pressure = 760 mm.

Relative humidity, %	0°C	20°C	35°C
50	100.30	101.17	102.94
60	100.23	100.93	102.34
70	100.18	100.70	101.77
80	100.12	100.47	101.18
90	100.07	100.23	100.60
100	100.00	100.00	100.00

found in practically the same locations. The separate effects of barometric pressure and relative humidity are shown in Tables 2 and 3 for sea water having a salinity of 35‰. It will be noted that, in waters in equilibrium with the atmosphere, relative humidities of less than 100% would result in apparent saturations $\left(\frac{O_2''}{O_2'} \times 100\right)$ of more than 100%, as would barometric pressures of greater than 760 mm. In this connection it is noteworthy that the zone of high oxygen saturation extending across the ocean at about 30°S. latitude coincides with the region of highest normal barometric pressures in the South Atlantic, as shown by Brunt (1939, Figs. 7 and 8). However, there is a poor correlation between apparent per cent saturations and the partial pressure of air in the atmosphere observed at the time of sampling. This might be expected, since the concentration of dissolved oxygen in surface samples would not be expected to respond immediately to changes in relative humidity and barometric pressure; it is more likely to be correlated with the integrated effect of these two parameters operating over some time preceding the sampling. Other factors, such as wind, the regime of warming and cooling and related differences between air and water temperatures, etc., would also be expected to have their effects on the oxygen content of the surface layer. The biological processes of photosynthesis and respiration and diurnal variations in them probably have an even more pronounced influence on the oxygen content at the moment.

The apparent oxygen utilization has been related to the regeneration of inorganic compounds of nitrogen and phosphorus and to *in situ* production of carbon dioxide by Redfield (1938, 1942) and others. The ratios in which oxygen is consumed and carbon dioxide, phosphate, and nitrate are regenerated have been reviewed by Richards and Vaccaro (1956). Since the consumption of oxygen has been estimated from equilibrium solubility data, $O_2' - O_2$, the new values of O_2' make revisions of these ratios necessary. Preliminary computations indicate that these corrections will be moderately small, but improved analytical methods for the other variables may make them important.

Recomputations of the values of the oxygen tension in the Gulf of Maine used by Redfield (1938) to examine the processes of oxygen exchange across the sea surface in that region indicate that his results are unchanged in a qualitative way, but their magnitude is appreciably altered. He evaluated the equation

$$P - p = P(O_2' - O_2)/O_2'$$

in which P is the oxygen pressure in the atmosphere, p the oxygen tension in the water, and O_2' and O_2 have their previous meanings. When $P - p$ is negative, the oxygen pressure in the water is greater than in the atmosphere, and oxygen will tend to pass from the liquid to the gas phase. Since O_2' is smaller than Redfield estimated, values of $P - p$ are smaller, in a positive sense, and it follows that conditions favoring the escape of oxygen from sea water are more pronounced and prevail

during a larger part of the year than Redfield estimated.

Since the errors in Fox's data are greater in low salinity water than in fully saline sea water, it is evident that the new data of Truesdale, Downing, and Lowden may be even more important in limnology and investigations of inshore waters and estuaries.

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Some of the Factors Affecting the Calibration Number of the Clarke-Bumpus Quantitative Plankton Sampler[1]

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ABSTRACT

Calibration values obtained by standard "field" calibration procedures are in error because a portion of the water encountered during the tow is rejected. A method is described by which the actual volume of water passing through the sampler is measured without disrupting normal flow characteristics around or through the meter. Depending upon net attachment and towing velocity, the percentage of water accepted varies from 90–94 per cent. An attempt has also been made to evaluate the effects of net clogging on calibration values.

INTRODUCTION

In the Spring of 1955 the Hydraulics Laboratory of the University of Washington made available facilities for the calibration of flow and volume meters commonly used in plankton sampling programs. At this time the writers decided to examine in some detail factors that effect the calibration values for the Clarke-Bumpus quantitative plankton sampler (Clarke and Bumpus 1950), and determine the significance of these effects in quantitative plankton sampling. Recently, Langford (1953) has challenged the quantitative validity of plankton samples taken with the Clarke-Bumpus sampler using nets smaller than number 10 mesh size. Edmondson (1956) as well as Clarke and Bumpus claim accuracy with the finer nets as long as the flow velocities through the meter are higher than 0.5 knot.

The standard means of calibrating the sampler by towing the unit without net over a measured water course is initially in error, because 100 per cent acceptance of the water encountered by the sampler is assumed during the tow (Clarke and Bumpus 1950). To overcome this objection the present writers designed a system for obtaining the volume of water flowing through the meter without altering flow conditions through or around the unit. Using this method, comparisons were made to determine the magnitude of error obtained by using field procedure calibrations (i.e., measured traverse tow). Variations in the assigned calibration value brought about by the attachment of different mesh-size nets were also observed, and an attempt has been made to estimate the effects of net clogging on the quantitative metering of water through the unit.

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METHODS OF CALIBRATION

To assign a calibration number to the Clarke-Bumpus sampler, one must know the volume of water that passes through the meter for one count registered by the counter. The simplest means of obtaining the volume per count, is to tow the sampler without a net over a measured water course. The total volume traversed is computed by multiplying the distance traversed by the total cross-sectional area of the meter, which assumes 100 per cent acceptance of all the water encountered during the tow. An alternate method involves housing the meter in a water-tight partition within a sluice-way (flume) so that all the water pass-

ing through the flume must pass through the meter. By this method water flow rates can be regulated, and the water exiting from the flume can be easily collected and measured. This method, however, imposes restrictions on the flow around the meter, while the difference in water levels on either side of the partition tends to force the water through the meter. Obviously, to obtain the true volume per count the volume of water passing through the sampler must be measured without interfering with normal flow patterns around or through the meter.

To do this the flume calibration method was modified in the following manner (Fig. 1). A Clarke-Bumpus sampler is suspended in towing position near the rear of the flume, not in a partition. A pipe seven inches in diameter is attached to the outflow end of the meter. The overall length of the pipe is six feet of which one foot extends past the end of the flume. The water level within the flume is maintained by a weir located at the outflow end. Water passing through the meter and pipe is conveyed to a large drum attached to weighing scales. Water flowing past the meter and over the weir is conveyed to a waste sump. Water flow rates within the flume can be regulated at the point of entry. Upon establishing a flow velocity within the flume the Clarke-Bumpus flow meter is attached directly to the pipe. A tight seal is made by using a brass conical clamp with rubber gaskets. The volume of water passing through the meter in a one-minute interval is carefully measured by conveying the outflow from the pipe to the weighing drum.

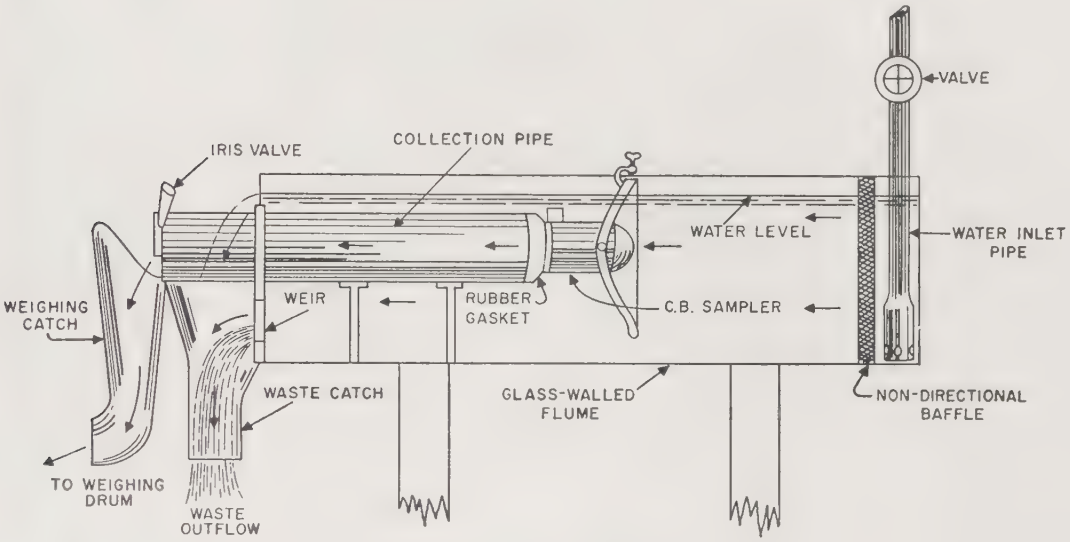

FIG. 1. The modified flume method for calibrating Clarke-Bumpus plankton samplers.

COMPARISON OF CALIBRATION METHODS AND THE EFFECTS OF NET ATTACHMENT

Calibration curves obtained by the three methods are shown in Figure 2. All curves show linearity between 40 and 120 counts per min. At flow rates below 40 counts per min. frictional effects within the instrument approach equality with the water forces, and the calibration values (vol/count) increase markedly. The flow-rate value of 40 counts per min.[2] corresponds to Clarke and Bumpus's value of 0.5 knots for the lower towing velocity limit of constant calibration. The upper limit given by them as 4 knots corresponds to about 450 counts per min. Exact determination of this value

[2] Referred to in Figures 2 and 3 as the "friction point". This point varies from sampler to sampler. On twenty samplers it ranged between 30 and 45 counts per min.

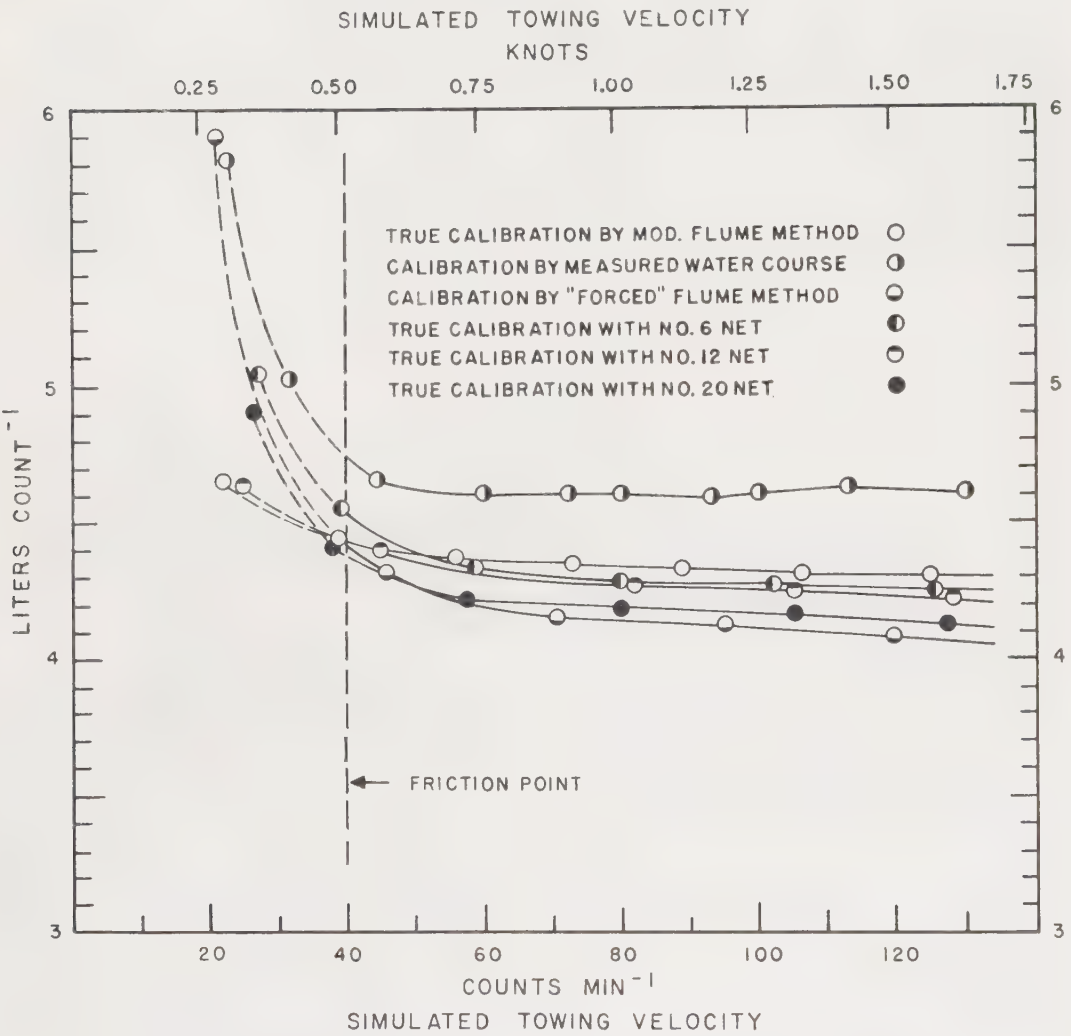

FIG. 2. Comparative calibration curves for the Clarke-Bumpus sampler.

TABLE 1. *Percentage of water accepted by the Clarke Bumpus sampler at various simulated towing velocities, with and without attachment of nets of various sizes*

Knots	Per cent water accepted			
	No net	#6 net	#12 net	#20 net
0.50	90	90	90	90
0.75	94	94	93	91
1.00	94	94	92	91
1.50	93	92	92	90

was impossible in the flume because of the high water velocities required. Comparison of the curves in Figure 2 shows that calibration values obtained by towing over a measured course are high, whereas low values resulted from using the flume arrangement where water is forced through the meter. The calibration obtained by the procedure described in this report is intermediate. The actual amount of water accepted by the sampler without net (Table 1) is approximately 94 per cent at simulated towing velocities between 0.75 and 1.50 knots.

A series of tests was made to determine the accuracy of calibration values when metering water through nets of different mesh sizes. Three sizes were chosen, numbers 6, 12, and 20, with actual mesh sizes

of 0.24, 0.12 and 0.07 mm, respectively (Fig. 2). The overall length of each net was 75 cm. Calibration procedure with nets attached was identical to that without nets. The nets were allowed to stream fully inside the collection pipe, and after every test they were thoroughly washed to obviate particular clogging. The attachment of the number 6 or 12 net decreases the calibration value by only 0.05 liter per count, whereas the finer number 20 net reduces the value by 0.10 liter per count at simulated towing velocities between 0.75 and 1.50 knots. The expected water acceptance by the sampler (Table 1) with number 6 or 12 net is about 93 %. The number 20 net decreases the acceptance to approximately 91 %.

Deviations from the true calibration value caused by net attachment or inaccuracies involved in measuring the exact volume of water passing through the sampler result in a maximum error of 15 %. Therefore, the quantitative planktonologist is safe in assuming a calibration value of 4 liters per count for the sampler as previously suggested by Clarke and Bumpus.

EFFECTS OF NET CLOGGING

As shown above it is possible to meter water accurately through fine plankton nets using the Clarke-Bumpus sampler. However, with progressive clogging the resistance to water flow through the meter is increased. In theory, at least, an efficient net not only traps organisms of a specific size range but also "clears" the straining area by transporting the organisms down the conical sides of the net into the collection cup. When coarse net sizes are used and organisms such as copepods are being trapped this clearing of the straining area functions quite properly. Conversely, with the use of finer mesh sizes, small filamentous forms are trapped on the sides of the net in such numbers that at times the total straining area is markedly reduced.

The reduction of flow rate through the Clarke-Bumpus sampler by net clogging was observed within the flume by introducing lake water containing a "bloom" of filamentous algae. Three different net sizes tested separately were allowed to clog until the meter wheel stalled. The number 6 net filtered continuously for thirty minutes with little reduction of flow through the meter. Two separate tests with the number 12 net stalled the meter after 15 minutes, and the number 20 net stalled the meter after periods of 4 and 8 minutes. Dye studies indicated that the number 20 net became progressively clogged from the cod end to the net mouth. When dye was introduced into the mouth of the sampler, it quickly passed through the non-clogged portion, not mixing with the water trapped in the clogged portion. As the net progressively clogged, water entering at the peripheral regions of the sampler was diverted around not through the sampler, thereby reducing the total intake diameter of the meter.

To examine the effects of resistance of water flow through the sampler, round wooden discs were carefully centered directly behind the outflow end of the current meter. By increasing the disc diameter it was felt that conditions somewhat similar to net clogging could be reproduced. Counts per min. with and without discs were carefully noted. As the total outflow area of the meter was reduced by increasing the disc size (Fig. 3), the slopes of the calibration lines changed considerably, indicating a deviation from the calibration values obtained without restrictions. The reduction of flow afforded by the number 12 and 20 net just approach the reduction afforded by the number 1 disc. The resistance to flow through the meter afforded by disc numbers 2 and 3 can be considered similar to situations occurring with extreme clogging. All deviations from the standard calibration values, induced by disc resistance, are magnified with the increases in the towing velocity. In terms of total net area clogged, the number 2 disc would be roughly comparable to having the lower half of the number 20 net fully clogged. By increasing the disc size to a point where the major portion of the outflow area of the meter is covered, as in the case of disc size number 4, the meter wheel will stop, and at times even commence, to run backward. This is due to the inflowing water at the center of the meter being

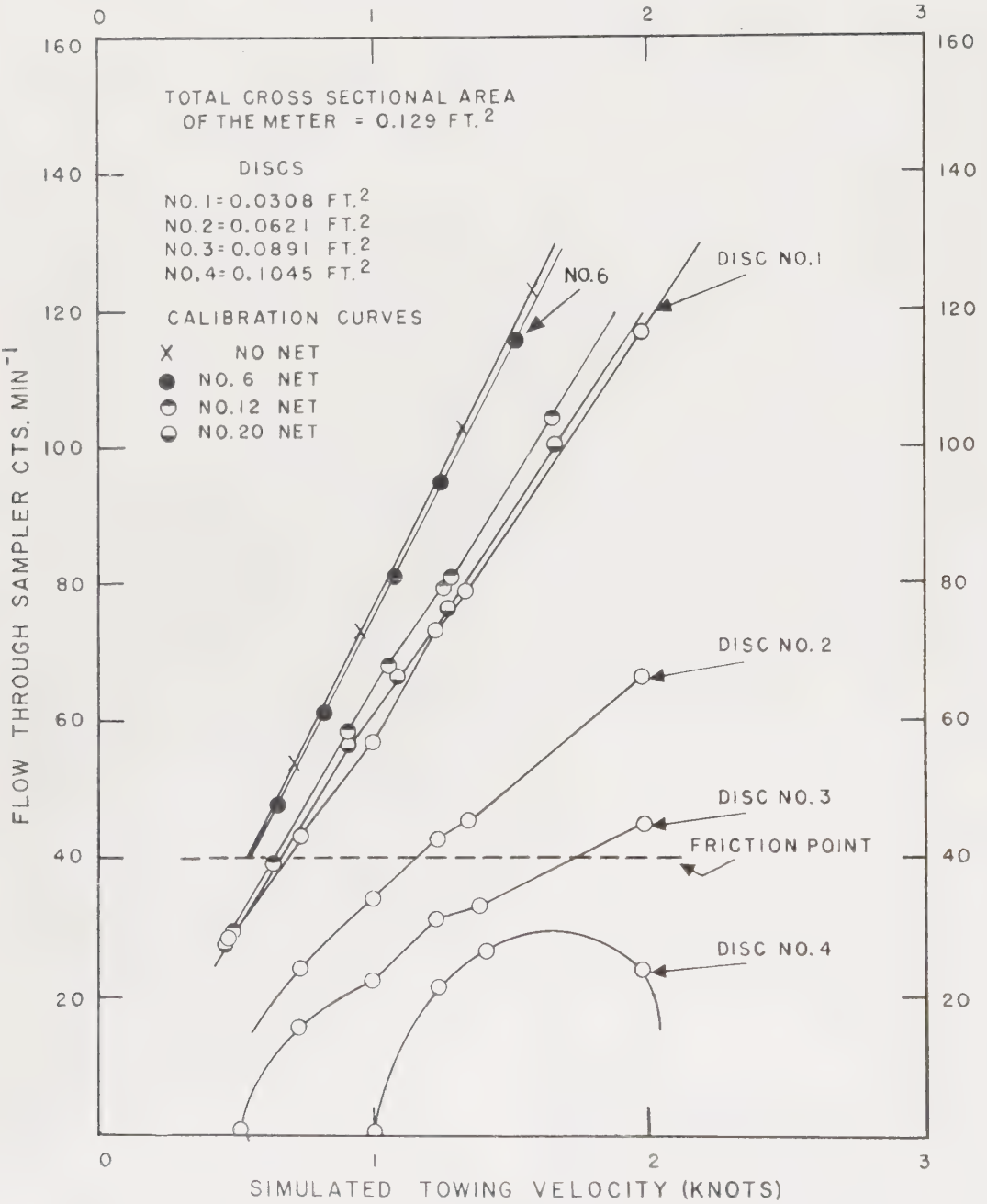

FIG. 3. The effects of resistance on the rate of flow through the Clarke-Bumpus sampler.

turned by the blocked net so that it flows back out near the outer diameter, thereby turning the metering propeller in reverse. An occurrence of this sort in the field is certainly due to a fully clogged net.

QUANTITATIVE TOWING WITH FINE NETS

Clarke and Bumpus state that as long as the flow velocity through the sampler and net are above 0.5 knot, calibration values are constant. Conversely, Langford (1953)

believes that nets finer than number 10 reduce the flow below the "friction point". Our data show that the initial towing velocity would have to be below 0.75 knot (Fig. 3) before the resistance of the number 20 net could reduce the flow below the "friction point" of 40 counts per min. At normal towing velocities of 1–2 knots, flow rates through the unclogged fine net are high enough to maintain a constant, accurate calibration value.

The slight decrease in the calibration value observed when nets are attached is the result of inflowing water being diverted over the peripheral regions of the propeller, turning it more effectively. Without net resistance, inflowing water passes through the central region of the meter not turning the propeller in this area effectively. Calibration values decrease with increased resistance brought about by net clogging until the "friction point" is reached. The calibration value then increases rapidly until the meter wheel stalls.

Obviously, extreme net clogging should be avoided. It is possible to estimate the "quantitativeness" of a particular haul where clogging is suspected by comparing the number of counts obtained for hauls with and without the net attached, keeping the towing time and velocity constant. If the number of counts obtained from the haul with net differs from the haul without by more than 40 counts per min., the haul should be considered quantitatively in error. In these cases quantitative hauls can probably be made by shortening the towing time. The writers have made some hauls only two minutes in duration to avoid severe clogging. The most satisfactory towing velocity is between 1 and 2 knots (80–145 counts per min.). At higher velocities a considerably greater portion of the water is not accepted by the sampler.

SUMMARY

Measurement of the actual volume of water passing through the Clarke-Bumpus sampler under normal conditions of flow past and through the meter gives values of approximately 94 per cent acceptance of the water encountered at simulated towing velocities of 0.5 and 1.50 knots. Reduction of flow rate through the sampler by a number 20 plankton net reduces the acceptance by 5 per cent. Changes in calibration values brought about by net attachment are not significant; however, serious error may result from net clogging. In this case, the calibration value (vol/count) decreases until the rate of flow through the meter approaches the frictional forces brought about by the metering mechanism. At this point the calibration value increases until the propeller stalls. Deviations from the assigned calibration value due to net resistance and clogging increases as a function of the towing velocity.

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Factors Influencing the Choice of Substratum in *Cumella vulgaris* Hart (Crustacea, Cumacea)[1]

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ABSTRACT

Dried sand which is put back into water is rejected at first by *Cumella vulgaris*. However, attractiveness of the dried sand increases with the time of immersion in water, the regaining of attractiveness proceeding more slowly in sand that had been dried in an oven at 55°C than in sand dried at room temperature.

In nature *C. vulgaris* prefers substrata with a median grain diameter of less than 160μ, and in the intertidal zone established populations occur predominantly below the 5 ft. level.

In sand predominantly finer than 150μ and in mud *C. vulgaris* feeds as a "deposit-feeder", while in sand predominantly coarser than 150μ it feeds as an "epistrate-feeder", that is, by scraping food off the surface of individual grains. If fractions finer than 150μ are thoroughly sieved, *C. vulgaris* cannot employ the latter feeding habit because the sand grains are too small for efficient individual handling by the mouth parts. On the other hand, deposit-feeding cannot be employed either, since the fine organic debris which in this instance serves as the source of food, has been removed by the process of sieving. Consequently, the attractiveness of the material is lowered markedly. However, if a sieving method is used in which the fractions finer than 150μ retain their content of organic debris, the material also retains its attractiveness. Sand grains coarser than 0.5 mm are too large to be handled in an efficient manner by the mouth parts of *C. vulgaris*.

The degree of attractiveness to *C. vulgaris* of a certain substratum must depend on the amount and the kind of food available. The food content seems to be one of the most powerful stimuli to which sand-inhabiting animals react in choosing substratum.

The factors influencing the choice of substratum in sand-inhabiting animals has has only recently become the subject of investigation through the work of Wilson (1952, 1955) and Jaegersten (1940). So far only polychaetes, the larvae of which are at first pelagic then settle and metamorphose, were studied experimentally. The fact that the larvae would metamorphose only in suitable substrata served as a convenient criterion for the suitability or non-suitability of a given substratum.

There can, however, be no doubt that also in adult animals the ability to choose between various types of sand, to reject one and to accept another, must be well developed. It can be assumed that this is particularly the case in crustaceans which leave their habitat for short excursions into the open water. Thus vagile animals like, say, cumaceans and amphipods, stand the risk of being carried far away from their original habitats. If this happens the animals must either be able to find a suitable substratum (be that now the original one or not) or they will perish. Whether or not these animals are exacting in their choice of substratum, and if so, what are the mechanisms that guide them is unknown.

These experiments represent a first step in the direction to finding out which properties of sand could possibly serve as clues to which sand-inhabiting animals might react in choosing substratum.

MATERIAL AND METHODS

All the experiments were carried out on *Cumella vulgaris* Hart[2], the most common cumacean in the littoral of Puget Sound and San Juan Island. The females and young used in the experiments were derived from False Bay on San Juan Island where they occur in tremendous numbers on those parts of the sand-flat that remain covered by standing water during low tide. The

[1] This study was carried out while the author was an I.C.A. Fellow in the Department of Zoology, University of Washington, Seattle.

[2] For the identification of the species I am indebted to Mrs. G. C. Carl, Victoria, B. C.

males were obtained from several beaches in the neighbourhood of Seattle, Washington, but most from "Golden Gardens," a beach within the city limits of Seattle, where *C. vulgaris* occurs quite regularly.

The animals were placed in dishes filled with the original substratum, either from Golden Gardens or from False Bay, and kept in a refrigerator at about 10°C (this being the mean water temperature of Puget Sound). There they thrived and even reproduced.

The experiments were simple experiments of choice. The animals were given in a petri-dish the choice between equal volumes of two kinds of substrata: an untreated and a treated one. Between the two substrata a strip was left empty on which the animals were placed at the beginning of the experiment. A glass plate covered most of the dish in order to prevent evaporation. The experiments were conducted in an illuminated refrigerator because of the sensitivity of the animals to changes of light (see below). The light-source was a small fluorescent lamp at a distance of 60 cm (6 foot-candles). Despite this set-up the animals seemed to behave in a normal way. Each experiment was carried out in duplicate and lasted for 24 hours. Forty or 50 specimens were used in each batch. At the end of the 24-hour period the dishes were taken out one after the other into the room and one of the two substrata quickly sucked into another dish by means of a large pipette. After the two substrata were thus separated the cumaceans were counted. This was done by shaking the dish and then pipetting the animals out of the water into which they were driven. The substrata were used only once, but the same batch of animals was used several times. After four or five experiments in a row the animals were put back into the dish in which the stock was kept. After a break of two or three days a new batch of 50 or 40 specimens was pipetted out of this dish (in which there were usually considerably more than 50 animals) and used for the next series of experiments.

One of the two substrata offered to the cumaceans was always the untreated "original substratum" which served as the reference point for the distribution of the animals at the end of each experiment. The "original substratum" came from places in which *C. vulgaris* occurred, either from the vicinity of Seattle or from False Bay. It was stored in large bowls in the same refrigerator in which the experiments were conducted. No cumaceans were allowed in these bowls. If the supply of sand decreased, the bowls were refilled little by little with fresh material from the beach, rather than replacing one batch of material by another. The substratum was frequently stirred and the water changed. All these precautions have to be taken in order to ensure homogeneity of this "original substratum." It is clear that in a series of experiments of choice the value (in my case the "attractiveness") of the reference point (the "original substratum") has to remain stable. There is no way of actually checking the degree of homogeneity of the material used, so that all I could do was to keep it under homogeneous conditions and well mixed. There should always be an ample amount of material in the bowl since variations of attractiveness are much more pronounced in small batches than in large ones. Some of my following conclusions are based on the assumption that the "original substratum" did not change its attractiveness conspicuously during the period the experiments were run. The nature of the treated substrata with which the "original" one was matched will be described in the respective sections below.

THE EFFECT OF DRIED AND REMOISTENED SAND

In preliminary trials it was found that dried sand is rejected invariably by *C. vulgaris*. If the original substratum was offered together with dried substratum that had just been put back into water almost all cumaceans would be found in the former. In order to investigate whether dried sand had lost its attractiveness permanently or whether it would regain it when remoistened and immersed in water for various periods, two series of experiments were undertaken. In one, sand was used that was dried at room

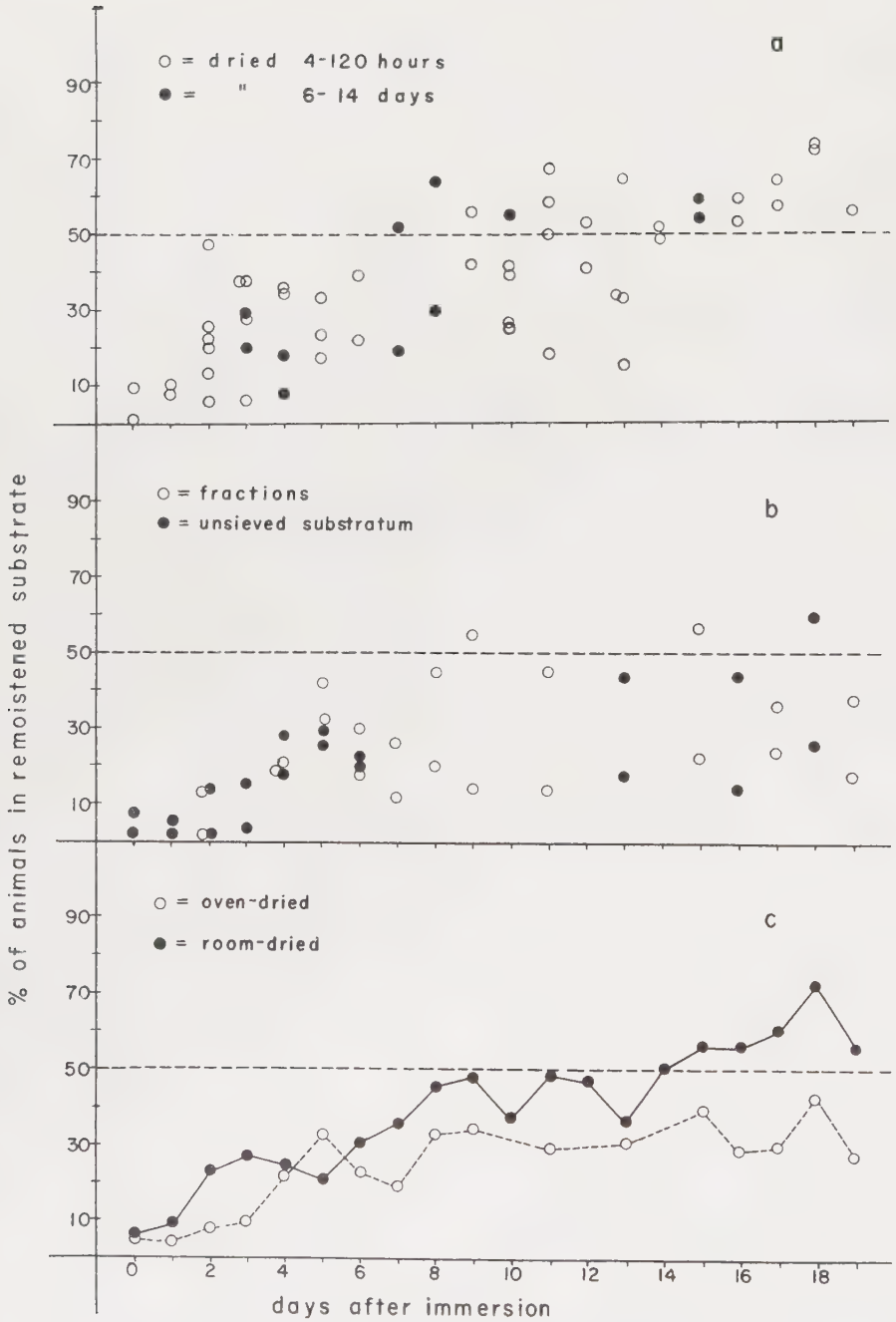

FIG. 1. Effect on *C. vulgaris* of dried sand after remoistening and reimmersion in water for various lengths of time, based on experiments in which the animals could choose between the treated and an untreated substratum. *a*. results with sand dried at room temperature for various lengths of time. Each circle represents one sample. *b*. results with sand dried at 50–55°C; fractions and unsieved sand were tested. Each circle represents one sample. *c*. mean values of *a* and *b*.

temperature mostly for 24 hours, but also for longer or shorter periods. It seems, however, that once the sand was dry it did not matter how much longer it was exposed to air (at least up to 14 days; Fig. 1a). In another series sand was used that had been dried in an oven at 50–55°C for 24 hours and then been stored at room temperature. In this series the dried substratum was used both in its original unsieved and in sieved form, since it was planned to investigate simultaneously the effect of grain size on the distribution of *C. vulgaris*. This approach, however, proved to be inadequate and the problem had to be tackled in a different way (see below).

In the experiments with dried sand the unsieved and the sieved sand seemed not to differ in their effect on *C. vulgaris* (Fig. 1b) Both series of experiments were carried out with females and with young in which the carapace was already well cuticularized. As substratum a medium find sand was used, the typical composition of which was as follows:

4760–2362μ....0.7%	1190–589μ.... 0.5%	295–149μ....76.9%
2362–1190μ....0.2%	589–295μ....20.7%	<149μ.... 1.9%

The dried sand was remoistened with and immersed in sea water that had been filtered through a Whatman filter paper no. 1. It was put into petri-dishes which were placed in the refrigerator used for all other operations. The water was changed frequently especially in the beginning in order to get rid of the dried salt on the sand grains. In each experiment the remoistened sand was matched with the original, untreated one as described below. The results are summarized in Figure 1a–c, the ordinate indicating the percentage of the cumaceans found in the *dried and remoistened* substratum. Theoretically a value of 50% means that both kinds of substratum were equally attractive. Figure 1a shows the results of all experiments with the room-dried sand, Figure 1b with the oven-dried sand, and Figure 1c gives the mean values of both.

It is evident that the attractiveness of dried sand increases with the time of immersion in water. There seems to be a significant difference between the room-dried and the oven-dried material as to the speed and completeness with which attractiveness is regained. The room-dried material begins to show an increase in attractiveness after two days of immersion, and after about eight days has reached a point where it is just as attractive as the original substratum. The oven-dried material, on the other hand, does not show a conspicuous increase in attractiveness until the fourth day of immersion, and it never (at least up to 19 days) became fully as attractive as the original substratum. This analysis is based on the average values of the two sets of experiments (Fig. 1c). There is, of course, a large range of variation within the individual tests.

In order to explain the effect of dried and remoistened sand on *C. vulgaris* we shall have to discuss the behaviour of the animal, which will be done further below. However, it should be anticipated that the degree of attractiveness of a given sand seems to be solely due to the extent to which it provides the right sort and the right amount of food. In the kind of substratum used in these two series of experiments *C. vulgaris* is an "epistrate-feeder," that is, it takes individual sand grains between its maxillipeds and maxillae and scrapes food off the surface of the grains by means of maxillulae and mandibles. Whenever one watches them the animals can be seen feeding, busily revolving sand grains with their mouth parts. The increase in attractiveness of the dried and remoistened sand shows that some food material, or the nutritive value of some food material, is increasing on the grains as the time of immersion increases. With other words, the drying killed or inactivated temporarily the sort of food stuff on which the cumaceans feed, but by remoistening the sand this foodstuff gradually appears again.

If examined under a microscope sand grains are found to be covered with a film of organic substance, consisting probably of bacteria and organic debris. Also a varying number of diatoms can be seen sticking to the surface. Which of these three components serves as the main source of food is unknown. Furthermore, it is not quite clear whether the food material that reap-

pears on dried and remoistened sand actually consists of those components of the organic film on the sand grains that survived the drying and are reactivated in water, or whether it is brought in by the water in which the sand is immersed. Since Whatman filter no. 1 is permeable not only to bacteria but also to small diatoms, the latter possibility certainly plays a role in reactivating the nutritive value of the sand. However, the difference between the room-dried and the oven-dried material seems to indicate that the regaining of attractiveness is at least to some extent due to the reactivation of the old film of organic material. This difference between the two kinds of dried sand might be interpreted in the following way: in the sand dried at 50–55°C more of the organic material was destroyed or killed, or its living components were more deeply inactivated, than in the room-dried material. Consequently it took longer to become reactivated and the degree of attractiveness after 19 days was not so high in the former as in the latter.

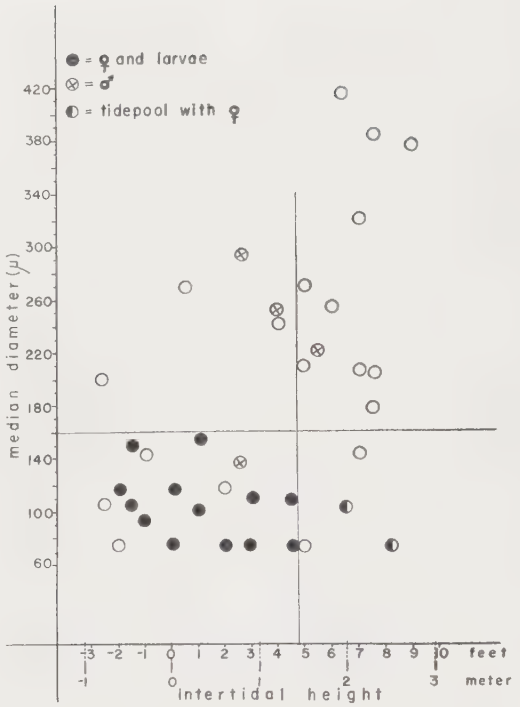

FIG. 2. Distribution of *C. vulgaris* in the intertidal of Puget Sound with respect to intertidal height and grain size. Empty circles indicate samples in which the species was not represented.

THE DISTRIBUTION OF *C. vulgaris* WITH RESPECT TO INTERTIDAL HEIGHT AND GRAIN SIZE

Thirty-eight samples were taken in the intertidal of Puget Sound and San Juan Island, the mechanical composition of each sample was determined, and the intertidal height noted. If the median diameter of each sample (according to the method given in Krumbein and Pettijohn 1938) is plotted against intertidal height it emerges (Fig. 2) that the samples in which females of *C. vulgaris* were present are mostly those that were taken at a height of less than 5 feet, and that consisted of sand with the median diameter less than 160μ. Since there exists a certain relationship between coarse sand and high altitude in the intertidal, the preference of *C. vulgaris* for the lower samples with finer sand is in itself complex. There is, however, some evidence that if the situation allows it both factors of grain size and desiccation might play an independent role in affecting the distribution of *C. vulgaris*. Of the four samples with fine sand which were situated higher than 5 feet, two contained the cumacean but both were from the tide pools on a sand flat (False Bay). One might therefore tentatively conclude that *C. vulgaris* would occur in fine sand above 5 feet only if the effect of desiccation is counteracted. On the other hand, there are 5 samples below 5 feet with the median diameter larger than 160 μ. None of them contained females or larvae of *C. vulgaris*, but in two of them single males were found. Thus the second tentative conclusion is that if the sand is too coarse *C. vulgaris* would not even occur in the lower intertidal.

The reason why females and males are kept separate in this discussion is that males are very active swimmers while females are not. Therefore, the presence of males, especially of few specimens only, in one sample does not necessarily imply that this is their proper habitat. They might have been carried in by water movements. On the other hand, if one finds a number of

females and larvae in a sample one can be certain that this constitutes their proper habitat.

THE EFFECT OF GRAIN SIZE

In order to find out in which way grain size could affect the distribution of *C. vulgaris* another set of experiments was undertaken. Fresh sand was sieved directly on the beach by flushing it with sea water through a set of Tyler Standard screens. The following screen numbers were used: No. 16 (openings 1190 μ), No. 30 (589 μ), No. 50 (295 μ), No. 100 (149 μ) and No. 200 (74 μ). The fractions were stored in petri-dishes in the refrigerator. In the experiments equal volumes of one of the size classes and of the "original," unsieved substratum were matched in the usual way. Two series of experiments were run. In the first, males from Golden Gardens were given the choice between the medium fine sand used in the experiments described previously, and fractions of the same sand. In the second series females and young from False Bay were given the choice between their original substratum (or one of the same composition) which is a very fine, muddy sand, and the same fractions as used in the experiments with the males. Thus the two series differed from one another with regards to two factors: firstly, in the sex of the animals used, and secondly, in the nature of the "original substratum," this being in one case medium fine, in the other very fine and muddy. The source of the original substrata used in the experiments was not always the same, but the composition of the batches was comparable, and the various samples without exception were derived from places in which *C. vulgaris* occurred. The results are summarized in Figure 3, the ordinate indicating the percentage of the animals which in each experiment was found in the sieved substratum. It should be noted that males and females in the two series of experiments behaved in very much the same way.

In experiments with the sand fraction which passed through the 295μ and was retained by the 149μ screen we find that both fraction and original substratum are of about equal attractiveness. Sand coarser than 295μ proved to be less attractive than

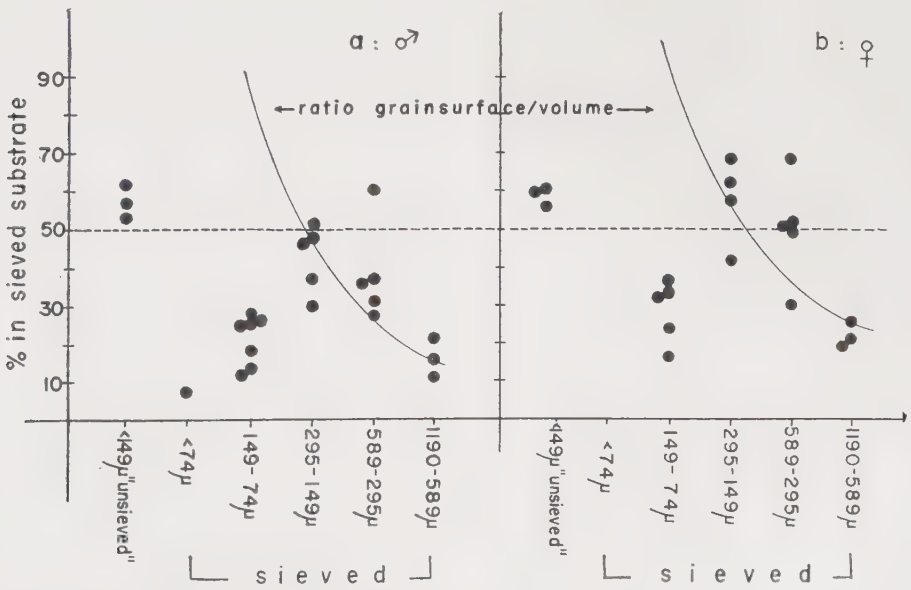

FIG. 3. Effect of various sand fractions on *C. vulgaris*, based on experiments in which the animals could choose between the sieved and an unsieved substratum. Superimposed is the curve for the ratio grain surface/volume if for the four coarser size-classes a median diameter of 111μ, 222μ, 444μ, and 888μ, respectively, is assumed. *a*. Experiments with males. *b*. experiments with females and young. For details see text.

the 149–295μ fraction. This decrease is especially obvious in the 1190–589μ fraction. The fraction that passed through the 149μ and was retained by the 74μ screen also proved to be less attractive than the 295–149μ fraction. The single experiment with sand finer than 74μ fits into this pattern.

The decreased attractiveness in the two size-classes coarser than 295μ might be just an effect of the decrease in the surface/volume ratio of the sand grains in these two fractions as compared with the 295–149μ fraction. This idea is supported by the fact that the decrease fairly closely fits the exponential curve which expresses the change in the surface/volume ratio. This ratio is indirectly proportional to the ratio of the grain diameters, and if a median diameter of 888μ, 444μ and 222μ is assumed for the three coarser fractions, respectively, it is 4:2:1. Why the attractiveness should be surface-dependent in these size-classes will become apparent in the discussion below. However, the decrease in attractiveness of the fractions finer than 149μ can obviously not be explained in the same manner. If attractiveness were entirely surface-dependent we would have to expect in these fractions a further increase of it as compared with the 295–149μ fraction, or at least not a drop. The reason for this deviation from the surface-dependence will be elaborated later on.

There is an inconsistency between these experimental results and the findings in nature. According to the experiments sand finer than 149μ ought to be less attractive than coarser one, whereas Figure 2 showed that *C. vulgaris* actually prefers fine sand. (It should be pointed out that the "median diameter" as used in Figure 2 cannot directly be compared to the size classes used in Figure 3. The "median diameter" is mostly smaller than the dominant size class of a particular sample.) While theoretically this inconsistency could have been explained in several ways, not necessarily involving the nature of the substratum, it was felt that whatever artificial characters the sand-fractions used in the experiments possessed they ought to be due to the process of sieving. It was for example possible that during sieving all the light organic detritus contained in the fine sand had been washed out and that this changed the attractiveness of the substratum. At first I did not believe in such a possibility since apparently it did not apply to the fractions coarser than 149μ. Moreover, I had previously run tests with coarser material from which emerged that even violent shaking of the sand in water and quick decanting did not alter the degree of attractiveness.

Since, however, all other attempts of explanation failed I decided to investigate the effect of sieving on the attractiveness of sand finer than 149μ. This was done in the following way. An area with very fine sand (about 90% finer than 149μ) was chosen and a large batch of this sand flushed with sea water through a 149μ and a 74μ screen. The bulk of the material passed through the coarser screen and quickly blocked the finer one since it piled up faster than it could be removed. Very soon the state was reached in which the 74μ screen was filled almost up to its rim with sand, and further sieving was impossible. The water, however, would still percolate, depositing on its way through the sand all the light organic detritus. What I got in the end was a great quantity of material finer than 150μ but still possessing the very fine organic and inorganic components that would have been washed out by an active process of sieving through a 74μ screen. This material was offered to *C. vulgaris* in the usual way. The results are shown in the left columns, Figures 3a and b labelled $<$149μ "unsieved." It is obvious that the material thus treated proved to be as equally attractive as the "original substratum," much more attractive than the fractions 149–74μ and $<$74μ after effective sieving. This proves that the process of sieving decreases the attractiveness of fine sand to *C. vulgaris*, while in sand coarser than 149μ it does not seem to have this effect.

DISCUSSION

If specimens of *C. vulgaris* are put in a dish with fresh substratum and left to acclimatize they will usually dig themselves

into the sand and remain buried until disturbed, whereupon they will leave the substratum and swarm towards the lightest side of the dish. They can be disturbed in several ways—by mechanical shock, by a sudden increase in light intensity, but also by changes taking place within the substratum itself. Thus if a population is left for a long time in a dish without renewing the substratum the animals will appear much more sensitive, and even the slightest touch of the dish or the opening of the refrigerator door will bring them out into the water. This goes so far until they stop digging in at all and remain in the water all the time, milling around despite the absence of other changes in their environment. Obviously the substratum has lost its attractiveness, perhaps has even become repellent. In general *C. vulgaris* appears to be more easily disturbed than *Diastylis rathkei* studied by Forsman (1938). Zimmer (1933:116) also seems to be referring to less easily disturbed species when he states quite generally: "Im Substrat eingegrabene Tiere reagieren aber nicht auf Beleuchtungsdifferenzen, weil offenbar der Kontaktreiz den Phototropismus uebertaeubt." The term "Kontaktreiz" (contact or haptic stimulus) is vague. What provides the *actual* stimulus that keeps cumaceans in their substratum? Is it really just the contact with the latter—in which case we would have to speak of thigmotaxis—or is it something else? The answer to this question would obviously be also part of the answer to the more general question with which we started: what are the environmental qualities on the basis of which sand-inhabiting animals are able to choose between suitable and non-suitable substrata?

Buried specimens of *C. vulgaris* seem to spend most of their time feeding. In fact, I have never seen a specimen which in coarse sand did not revolve sand grains with its mouthparts. This was also noted by Foxon (1936) for *Iphinoe trispinosa*, *Pseudocuma longicorne*, and *Lamprops fasciata*. Foxon states, "As soon as one grain is finished with, the process is repeated with another." Now it seems that this is continued as long as there are unused sand grains within reach of the animal's maxillipeds (or first pereiopods). When one spot has been exploited the animal "leaves that spot and swims away to a fresh site, where it settles down and begins to bury itself again." This mode of changing feeding-sites holds both for Foxon's three species and for *C. vulgaris*. Forsman, however, reports that *Diastylis rathkei* would seldom swim from one site to the other, but instead plough through the substratum. Although this mode of propagation does occur occasionally in *C. vulgaris* it certainly is less important than swimming.

If this interpretation of the feeding behaviour of *C. vulgaris* and of its mode of changing feeding sites is correct, the obvious consequence of it is that the length of time a certain specimen will remain buried at a given site depends on the amount of food to be found there. The fewer sand grains covered with organic material it can get hold of with its maxillipeds, or the less nutritive substance it can scrape off per grain with maxillae and mandibles, the sooner it will have finished its exploits at a given spot and swim away to find another. This is the only assumption we need to explain the results of the experiments dealt with above.

Let us consider an experiment of choice in which the untreated, "original" substratum is matched with a dried one that had just been remoistened. The dried substratum is almost totally depleted of nutritive material, this having been killed or inactivated in the process of drying. At the start of the experiment the animals will mill around at first and then settle down at random. If they happen to settle on the dried substratum they will find no, or hardly any, food and consequently will leave the spot very soon again. If they settle on the untreated substratum they will find plenty of food at each spot and remain there for quite a while. The result of such behaviour is that the animals will gradually aggregate in the untreated substratum. This is precisely the mechanism responsible for the kind of directed movement called "ortho-kinesis" by Fraenkel and Gunn (1940). The directing force is not a definite goal but the variation in linear velocity of

the animals. A population will seem to abandon a place in which the velocity of its members is high, and to aggregate in one in which their velocity is low. This appears to the observer as if they were "repelled" by the former and "attracted" by the latter substratum.

The results of all the experiments are based on these ortho-kinetic movements of *C. vulgaris*. Whenever in a dish a significantly greater portion of animals aggregated in one-half of the substratum, this was due to the relative abundance of food in this half as compared with the other one, which difference in its turn caused the animals to remain buried for longer periods in the former than in the latter. Thus the experiments with dried sand show, as was already anticipated, that the dried and remoistened sand in the beginning must have been almost completely devoid of nutritive material. The amount of the latter increased as the time of immersion increased. This process got under way more slowly in oven-dried than in room-dried material.

As to the experiments with different size-classes of sand it must be concluded that the fraction 149–295μ provided equally much food (or slightly more in females?) as the "original substratum," but all other fractions provided less than the 149–295μ fraction. As far as the coarser size-classes (295–589μ and 589–1190μ) are concerned the results can be explained on the grounds that the coarser the grains the lower is their surface/volume ratio, which is to say that per burying site the animals would have fewer surfaces at their disposal in coarse than in fine sand, and this means less food since amount of food and area of grain surface are directly proportional.

There comes, however, yet another factor to bear on the problem and this is the proportion between grain size and the size of the mouth parts of *C. vulgaris* (if we remember that the animals feed by revolving individual sand grains with their mouth parts, in this way scraping food off the surfaces of the grains). Figure 4 shows the size relationship between a fully grown female of *C. vulgaris* and the fractions of sand used in the experiments. The assumption appears to

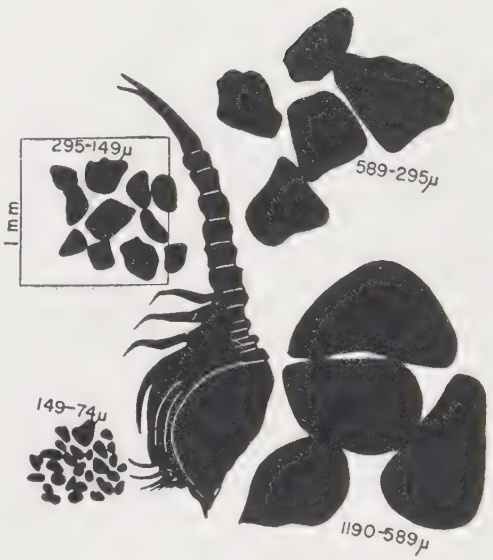

FIG. 4. Mature female of *C. vulgaris* and sand fractions used in experiments to show size relationship.

be reasonable that the coarsest grains are too large to be handled in an efficient manner by the mouth parts of the animals. This would be an additional explanation for the very distinct drop in attractiveness that occurs between the 295–589μ and the 589–1190μ size-classes. The finest grains, on the other hand, give the impression of being too small for efficient individual handling by the mouth parts of *C. vulgaris*, and this is probably the sole explanation for the unexpected drop in attractiveness that occurs between the 149–295μ and the 74–149 size-classes.

Now in order to explain the high attractiveness of the *unsieved* material finer than 149μ we have to introduce the well-known fact that in cumaceans there exist two modes of feeding. So far we have mentioned only one of them, *i.e.*, the "epistrate-feeding" ("Sandlecken" in German literature; see Remane 1933) in which individual sand grains are worked over as described above. In the coarse and medium-fine sand dealt with so far only this mode of feeding occurs. It was also described by Zimmer (1933) and Foxon (1936) for sand-inhabiting forms like *Iphinoe trispinosa*, *Pseudocuma longicorne*, and *Lamprops fasciata*. However, in mud-inhabiting species such a feeding behaviour

obviously would not work and in this case the animals are plain "deposit-feeders," that is, with their first pereiopods they shovel in masses of material which according to Forsman is sorted by the third maxilliped and the suitable components taken to the mouth parts. A question of minor importance is whether this mode of feeding is assisted by a filter mechanism. Dennell (1934) described such a mechanism in detail for *Diastylis bradyi*, but according to Forsman no filtering occurs in *Diastylis rathkei*. It is not easy to distinguish between pure "shoveling in" of material, and sucking and filtering. Probably both mechanisms occur together since a) the "shoveling" can be readily observed, and b) the respiratory current will inevitably take in soft material from the immediate neighbourhood of the buried animal and suck it right through the mouth parts where the setae on maxillipeds and maxillae will act as a filtering device.

We have now all the facts we need in order to explain the behaviour of *C. vulgaris* in the experiments with different grain sizes. In size-classes consisting of grains large enough to be handled individually *C. vulgaris* is an "epistrate-feeder" or "Sandlecker." Consequently, the sieving or shaking and decanting of the material had no effect on the attractiveness of the latter. As the material gets finer the animals cannot any more handle the sand grains individually, and since the process of sieving has removed all the light organic detritus they have fallen, so to speak, between two stools: their epistrate-feeding cannot be applied any longer because the individual grains are too small, and the deposit-feeding cannot be applied because there are no fine deposits left. Consequently, the substratum has lost its attractiveness for them, as is plainly to be seen in Figure 3. If in fine sand the light organic detritus is prevented from being washed out by the method described above, the animals switch entirely to the mode of deposit-feeding, and the substratum retains its attractiveness. In this case the degree of attractiveness is not any longer surface-dependent as it is in coarser fractions. It seems as if both modes of feeding are about equally efficient, for if the animals are offered a coarse, but not too coarse, and a fine, unsieved substratum they show in both—in the language of Fraenkel and Gunn—the same linear velocity, that is, the two substrata appear to be equally attractive.

From this we ought to be able to predict that *C. vulgaris* will occur both in very fine sand and mud where it will be a deposit-feeder, and in somewhat coarser sand (in which the 295–149μ fraction is well represented) where it will be an epistrate-feeder. Natural substrata are, of course, always mixed, but it seems as if this prediction on the basis of experimental data could be borne out by observation. A median diameter of 74μ in Figure 2 characterizes very fine sand or muddy habitats, while the median diameter of 160μ which marks the upper limit of distribution for established populations of *C. vulgaris* comes fairly close to characterize a sand in which the 295–149μ fraction is dominant, followed by the 589–295μ-fraction. Very fine sand which at the same time is devoid of organic detritus (a situation which is rare and which was never met with in my area of investigation) should be a habitat unsuited for *C. vulgaris*.

CONCLUSION

It seems to be possible to state in a very general manner that the degree of attractiveness to *C. vulgaris* of a certain substratum must be dependent on the amount, and the sort, of food available. This factor exerts its influence either directly or indirectly through the size of the sand grains since from both too large (larger than 600μ) and too small (smaller than 150μ) grains food cannot be extracted efficiently by the species under consideration.

The absence of food in a substratum acts as a repellent stimulus, seemingly driving the animals out into the water. This is emphasized by the observation that a population of *C. vulgaris* which has been kept in a small batch of substratum over a long period will gradually—as it diminishes the supply of food—leave this substratum and swim around in the dish. Finally the animals will stop digging in completely and

settle on the ground only for short periods between their spells of swimming. Thus the effect of the absence or presence of food and the corresponding mode of behaviour in the animals might be the sole means by which *C. vulgaris* in nature distinguishes between suitable and non-suitable substrata. It can be envisaged that the animals after an excursion into the open water will settle at random, testing the substratum for its nutritive value, taking off if it is found to be unsuitable, but staying if it proves to be suitable.

It is interesting to note that the latest experiments of D. P. Wilson (1955) concerning the metamorphosis of larvae of *Ophelia bicornis* have yielded very similar results. Wilson found that the factor inducing metamorphosis in this polychaete larva "is the presence on sand grains of living microorganisms, such as bacteria. . ." The difference is here that the larvae themselves do not feed. However, it might be possible to speculate that the food requirements of the adult are anticipated in the reactions of the larvae.

Thus, the food content of a certain substratum seems to offer itself as one of the most powerful clues to which sand-inhabiting animals will react in choosing substratum. It can also be looked upon—in the language of the modern behaviourists—as a releasing mechanism which evokes a definite behaviour pattern in the animals concerned.

SUMMARY

These experiments were undertaken in order to find out which properties of sand could possibly serve as clues to which sand-inhabiting animals might react in choosing substratum. In the experiments a choice between untreated and treated substrata was offered to a batch of cumaceans, *Cumella vulgaris* Hart.

Dried sand which is put back into water is rejected at first by the cumaceans. However, attractiveness of the dried sand increases with the time of immersion in water, the regaining of attractiveness proceeding more slowly in sand that had been dried in an oven at 55°C than in sand dried at room temperature. This was explained by the assumption that either more of the organic material on which the animals feed was destroyed or killed, or that its living components were more deeply inactivated in the oven-dried than in the room-dried sand.

In nature *C. vulgaris* prefers substrata with a "median grain diameter" of less than 160μ, and in the intertidal established populations occur predominantly below the 5 ft.-level.

In experiments with different grain sizes the 149–295μ-fraction proved to be more attractive than either coarser or finer fractions, provided the material had been sieved thoroughly. As to the diminished attractiveness of the coarser fractions, this is explained by two assumptions: 1) the coarser the grains the lower is their surface/volume ratio, which is to say, the less food is available to the animals per burying site since they feed on material that sticks to the surface of the grains; 2) the coarsest grains (larger than ½ mm) are too large to be handled in an efficient manner by the mouth parts of the animals. As to the diminished attractiveness of the finer fractions the following observation is relevant. In sand predominantly coarser than 149μ *C. vulgaris* feeds as an "epistrate-feeder" by scraping food off the surface of individual grains, whereas in sand predominantly finer than 149μ and in mud it feeds as a "deposit-feeder." In the fractions smaller than 149μ which were thoroughly sieved *C. vulgaris* cannot employ the former feeding habit because the sand grains are too small for efficient individual handling by the mouth parts. On the other hand, deposit-feeding cannot be employed either, since the fine organic debris which in this instance serves as the source of food has been removed by the process of sieving. If a sieving method is used in which the fractions finer than 149μ retain their content of organic debris, the material proves to be just as attractive as the 295–149μ fraction.

In conclusion it can be stated that the degree of attractiveness to *C. vulgaris* of a certain substratum must be dependent on the amount, and the sort, of food available. The food content seems to be one of the most

powerful clues to which sand-inhabiting animals will react in choosing substratum.

The search for suitable substrata is affected by the mechanism of ortho-kinetic movement which keeps the animals agitated and swimming as long as they are in contact with an unsuitable substratum; not until they have found a suitable substratum will they settle down and come to rest. To an observer this gives the impression that the animals are "repelled" by the former and "attracted" by the latter.

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Factors That Control Species Numbers in Silver Springs, Florida[1]

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ABSTRACT

The effect of productivity on species variety has been studied by counts of diatom species on glass slides at a high production and a low production station within Silver Springs. Species variety has been presented in a measure that is apparently independent of sample size. This measure is based on the linear increase of accumulated species with logarithmic increase of individuals counted. Diatom productivity was measured by the rate of chlorophyll accumulation. The poor station accumulated diatoms and chlorophyll slowly and was characterized by a large species variety during most of the experiment. The rich station accumulated diatoms and chlorophyll rapidly and was characterized by a rapid decrease in species variety as the density of the population increased. These results indicated that species variety was decreased by conditions of high productivity, possibly through the action of high densities and coactions. In addition, other factors that affect species variety were classified and discussed.

INTRODUCTION

This study was carried out in Silver Springs, Florida, but the ideas which instigated it were arrived at during 1952–54 from a study of the salps in a series of plankton samples collected by the Pacific Oceanic Fishery Investigations of the United States Fish and Wildlife Service in epipelagic waters of the Central Pacific Ocean. Observations on these salps led to the hypothesis presented below. The most pertinent observations follow. In most of the samples studied many species of salps were taken with little predominance of any one species. In one sample, however, there were both a far greater total salp quantity and a predominance of one species of salp, only a few others being taken and these in insignificant quantities. All salp species apparently occupy similar niches ("the 'niche' of an animal means its place in the biotic environment, *its relations to food and enemies*"—Elton 1927:64). They also appear to be subject to the same environmental conditions, thus apparently are ecological equivalents.

Observations made by other investigators are also pertinent here. Students of the marine plankton of high latitudes have described it as "monotonous", consisting of one or a few species in each plankton sample. Most descriptions of the plankton of low latitudes, however, emphasize the great variety of species with little or no predominance by any one species (cf. Steuer 1910: 601–4, Russell and Yonge 1936:123–6, Dakin and Colefax 1940:27–34). The same relationship has been long known for tropical vs. temperate and polar terrestrial biota. (This problem was recently well stated by Carr 1956:103–8.) Another pertinent observation discussed by Steuer, Dakin and Colefax, and Russell (1934) is that productivity in the tropics, in waters influenced by land drainage and in regions of upwelling, may equal or even exceed that of high latitudes, and again, this has been long known to be true of terrestrial biota (*e.g.*, Elton 1927: 105, Hesse *et al.* 1951:483–4).

If these observations are considered together, it appears that in epipelagic waters with relatively great quantities of nutrient chemicals, production of the plankton is great in quantity but trends toward few species of organisms, and that in epipelagic waters with relatively small quantities of nutrient chemicals, the plankton is small in quantity and trends toward many species of organisms. Occasionally in tropic waters swarms of plankters appear, consisting of few

[1] This investigation was aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Florida (NR 163-106).

species of organisms and a relatively great quantity—apparently productivity is high and species numbers few, even in the midst of impoverished waters, under enriched conditions. In plankton tows from impoverished waters many species of organisms are taken together that are apparently ecological equivalents, and this is evidently not true of enriched waters.

It was postulated from these observations that if productivity is low and other factors constant, species variety is high while numbers of individuals are few, and conversely if productivity is high and other factors are constant, species variety is low while individual numbers are great. In other words, the species variety is an inverse function of the community productivity. This led to postulates on coactions, particularly competition, which are discussed below. While investigating this hypothesis, it was found convenient to investigate generally the factors that control the numbers of species in Silver Springs, at least to the extent of classifying them.

There is only sporadic mention in the literature of factors that control the species numbers of an area. Among these factors, one of the most commonly mentioned is isolation. For example, the species numbers of oceanic islands have been considerably increased with the appearance of man, simply because many species are unable to reach these islands without man's help (cf. Hesse *et al.* 1951:622, Gressitt 1954:127 ff.). Isolation is regarded by Brooks (1950) as an important factor influencing species variety in ancient lakes. Other factors mentioned in the literature may be classed under one heading (Hesse 1943:789) as proximity to the general optimum. For example, temperature is an important factor influencing the species variety of blue-green algae in the Yellowstone area as reported by Vouk (1950). Other factors that might be listed here are numerous, including such things as hardness of water (Smith 1950:21), extent of pollution (Patrick *et al.* 1954), food (Hesse 1943:790), etc. Some biotic factors that might be mentioned are competition, grazing, predation, and cooperation.

In addition to these factors, two others should be mentioned which were examined in detail here. These are time or age, a successional phenomenon, and productivity, a biogenic phenomenon. As shown below, they are apparently of great importance in the species variety of Silver Springs, and presumably of all areas.

In Florida there are many large springs in which conditions of the environment are relatively constant (Ferguson *et al.* 1947, H. T. Odum, 1953), and these springs are therefore usable as natural laboratories. I was particularly fortunate to be able to test the above stated ideas under the unusually constant conditions of Silver Springs, working with diatoms which are numerous on larger plants and man-made structures in the spring.

I should like to express my gratitude to the following individuals for criticism and encouragement: L. D. Tuthill and R. W. Hiatt of the University of Hawaii, R. E. Coker of the University of North Carolina, and especially H. T. Odum of Duke University with whom much stimulating discussion was held during the summer of 1955. I wish also to thank the management of Silver Springs for permission to carry out this work there.

METHODS

It was thought best to use for this study a group of organisms which were common, could be fairly easily counted and identified, and on which productivity could be estimated. Diatoms were found to best fill these requirements, especially since they attach to microscope slides and since they remain permanently identifiable after removal from the water. For the diatom study, then, slide boxes were used by removing the covers and backs; 8 slides were placed in each box and the whole was covered with ¼″ mesh hardware cloth. A group of these boxes were placed at a number of stations in Silver Springs by suspending them from stakes at approximately one foot below the surface. At various time intervals two slides were removed from each station and later examined at the laboratory in Gainesville.

In the laboratory chlorophyll was removed

and estimated quantitatively by placing the slide in acetone and measuring the resulting solution with a spectrophotometer (the method of Richards with Thompson 1952). The slide was allowed to dry and placed on the microscope; immersion oil was added directly to its surface, and the diatoms were identified and counted. The principal reports used for identification were those of Boyer (1916), Hustedt (1930) and Tiffany and Britton (1952).

After a period of study, during which the various species were learned and errors in technique were overcome, new sets of slides were placed at the various stations, and two (rarely one) slides were removed at different intervals. Ten microscopic fields were selected at random and counted on each slide; thus an equal area was studied on each slide, so that direct comparisons could be made. Each microscopic field was approximately 0.021 mm^2 in area, so that the area counted for each slide was approximately 0.21 mm^2. For certain purposes the two slides taken from each station were averaged as seen below.

The stations used for the study at Silver Springs were selected for presumed differences in productivity. Two stations are reported on here: the high production one is located near the main boil of the spring, with a relatively strong current and with much light present; the low production station is located in a side pool which has little current and, as it is under a projecting tree as well as under accumulated floating *Sagittaria*, relatively little light.

In order to best illustrate the differences between the stations, graphs were made with the counts (cumulative individual numbers) plotted against the species variety (cumulative number of species) following the method of Vestal (1949) with some differences. The curves of Vestal, Oosting (1953), and others are species-area curves, whereas in the present paper equal areas were compared and hence the curves are species-individual curves. Rice and Kelting (1955) noted that Vestal's use of a semilogarithmic species-area curve (areas placed on a logarithmic scale) may be of real value for adequacy of sampling. Rice is at present attempting to clarify this statistically. Here it is assumed that this technique is valid for species-individual curves considering that in all cases the area counted was the same.

RESULTS

Figures 1 through 10 show the species-individual curves obtained from counting 10 fields on slides from two stations—the high production area or near boil station and the low production area or side pool station. The quantity of chlorophyll, also in these figures, is, in addition to total numbers, presumably a valid measure of the quantity of plants and therefore of primary productivity. The effect of time is also evident in these figures, which illustrate slides taken from the water at various intervals from 7 days to a maximum age of 335 days.

Figure 1 shows that, at first, slides from the two stations were very similar as regards the species-individual curves. At 7 days of age there were many species and few individuals at both the rich and poor stations. Figure 2 (16 days) shows the beginning of a separation in the curves from the two stations. There were still, however, few individuals and many species at both stations. The chlorophyll quantity also is beginning to show considerable difference between the two stations (0.128 mg rich station vs. 0.005 mg poor station).

Figure 3 (28 days) shows the first clearcut separation between the curves from the two stations. The number of individuals at the poor station was still low and the species variety remained high. At the rich station, however, the number of individuals increased greatly and, at the same time, the species variety decreased. In this case then, the most critical period at the rich station was presumably somewhere between 16 and 28 days for both a considerable increase in numbers of individuals and decrease in species variety. No such change is yet seen at the poor station, which up to 28 days remained rather static. These changes which occurred at the rich station are reflected in the tremendous jump in chlorophyll quantity, to more than 0.3 mg,

whereas the chlorophyll quantity at the poor station remained below 0.01 mg.

At approximately 50 days of age (Fig. 4) the separation between the curves from the two stations increased further. Again the poor station remained fairly static with many species and few individuals, whereas the rich station continued to be dynamic with considerable increase in numbers over Figure 3 and with considerable reduction in species variety. The chlorophyll difference between the two stations was still great, although the quantity at the rich station was less than that at the same station at 28 days of age (Fig. 3). This is perhaps at least partially explainable in this way: the slides represented by Figure 4 (rich station) were taken up on the 8th of September, probably entering into a period of less light with the approach of autumn, whereas the slides represented in Figure 3 (rich station) were taken up on August 18, still in the summer.

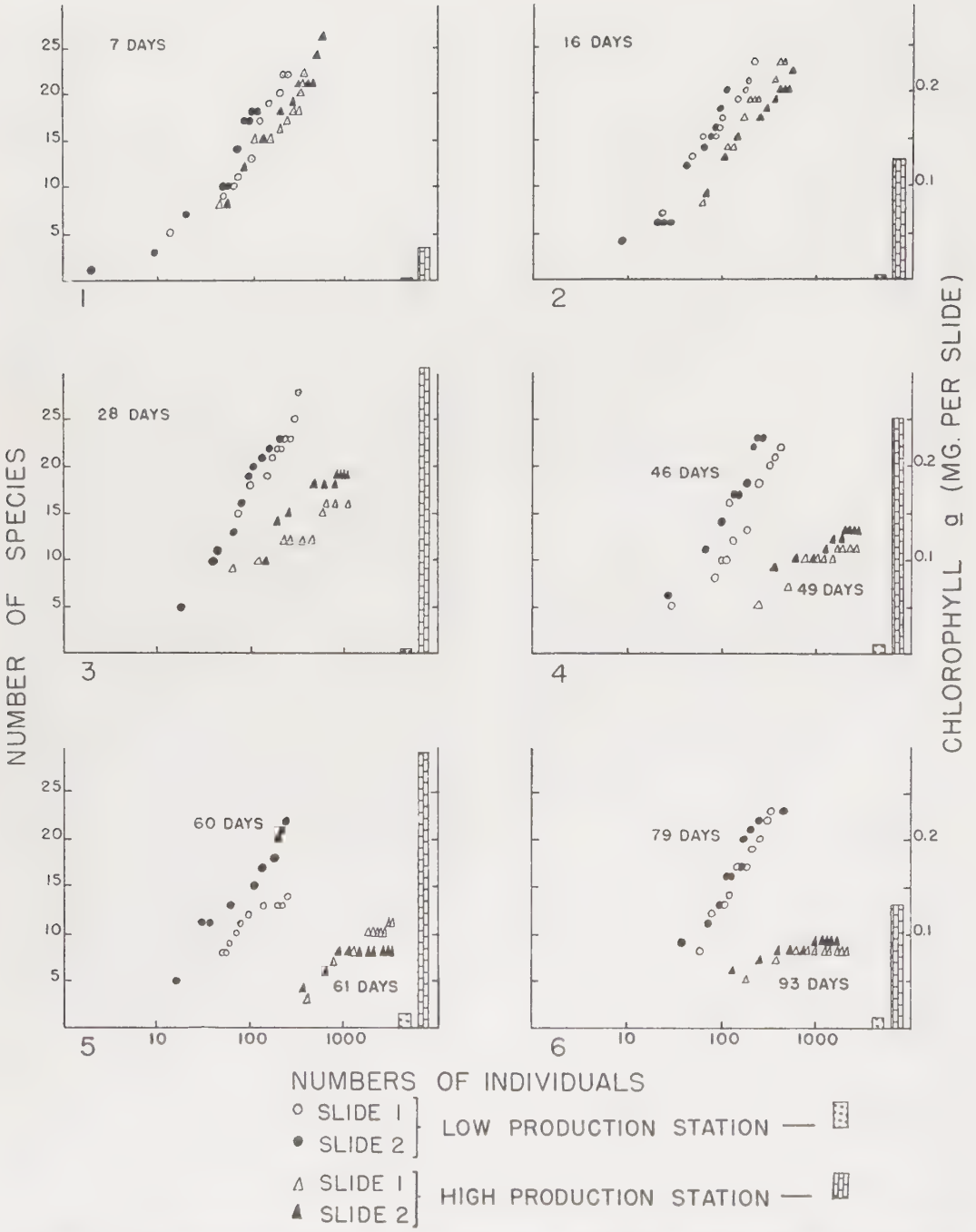
Figures 5 and 6 emphasize a continued change at the rich station as opposed to continued fixity at the poor station in regard to the species-individual relationship. At the rich station the species variety was further reduced along with a continued increase in numbers as shown in Figure 5. Figure 6 reveals a decrease in numbers over Figure 5 at the rich station, but the dominant species changed. After 61 days at the rich station, a small species, *Achnanthes lanceolata*, was the dominant species; whereas after 93 days, *Cocconeis placentula*, usually considerably larger than the former, was the dominant form. Thus, although numbers were less at 93 days, the volume of the individuals was perhaps no less. The chlorophyll quantity increased at the rich station at 61 days (Fig. 5) over 49 days (Fig. 4), whereas at 93 days (Fig. 6), it was far lower than at most previous determinations. The latter situation is probably best explained by the lesser light in Autumn (October 22). The difference in chlorophyll between 49 and 61 days was small and perhaps merely individual variation; it is probably without significance.

At the poor station the numbers remained low, the species variety high, and the chlorophyll quantity low at both 60 days of age (Fig. 5) and at 79 days of age (Fig. 6). Differences in chlorophyll quantity at the different ages were so slight that they appear to be merely individual variation, even though there is a tendency for reduction in chlorophyll with the approach of winter (Fig. 6, poor station, represents slides removed on November 10, 1955).

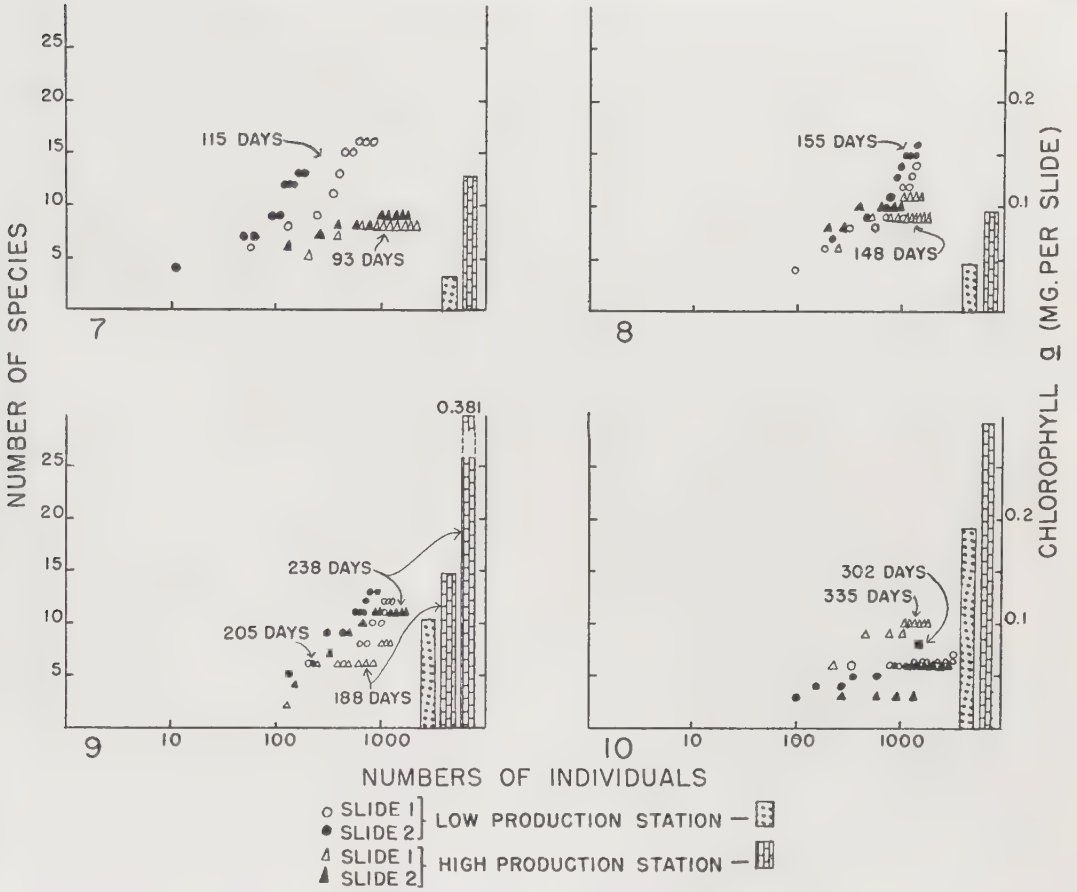
Figures 7 through 10 reveal a continued fixity of the species-individual relationship at the rich station, probably indicating that a climax has been attained here after the rapid buildup during the earlier period. The poor station gradually changed until it too revealed a reduction in species variety and an increase in individual numbers. Thus both the rich and the poor station reached an apparent climax during the period of the experiment, the former rapidly and the latter much more slowly. In this connection it should be mentioned that the poor station was covered by a mass of floating *Sagittaria* every time it was visited until December, 1955 (age 115 days), when it was noted that no floating mass was above the slide box. A mass did not cover the slide box at any time since then.

There is apparently some discrepancy in the trend at the rich station, in that the species variety increased slightly at age 148 and 188 days (Figs. 8 and 9) over that at age 61 and 93 days (Figs. 5, 6, and 7). The difference, however, is slight enough, I think, to be accounted for as individual variation. Another apparent discrepancy is seen in the chlorophyll quantity, especially in Figure 9, but this probably is due to the increased light associated with summer (the very high determination having been made from one slide removed on June 20, 1956), and individual variation.

It thus appears evident as illustrated in these figures that two factors are of prominent importance in the species-individual relationship: time and productivity. Although there is variation in the picture afforded by this relationship, there is obviously a distinct tendency for the species variety to decrease while individual numbers increase but only when enough time has elapsed to permit such a change to take place. The length of time needed for this



FIGS. 1-6. Diatom species-individual curves from slides left in Silver Springs, Florida, for different lengths of time as indicated in figures. Chlorophyll quantity (average of 2 slides from each station) is indicated on right.



FIGS. 7–10. Diatom species-individual curves from slides left in Silver Springs, Florida, for different lengths of time as indicated in figures. Chlorophyll quantity (average of 2 slides from each station except the high production station in Figure 9, in which the chlorophyll quantities represent one slide each) is indicated on right.

apparent climax appears to depend on productivity. It is probable that if productivity remained low enough, a climax would never develop, the slide community remaining permanently in a sub-climactic state.

DISCUSSION

As a result of the data and ideas accumulated from this study, attempts to classify all factors that influence the number of species in an area have been made. Two principal factors appear to do this, the history of the area and the proximity of the area to the general optimum. Under the former are placed isolation, new species formation (genetics) and the time factor, age of the substrate or of the medium. Under proximity to the general optimum are included various environmental factors, both abiotic and biotic, such as temperature, water, chemicals in solution, predation, competition, etc.

The history of an area may considerably influence the number of species present. Species that could live in the area may not have been able to get there, and thus isolation is undoubtedly of importance in many areas, especially among those organisms with poor means of distribution. If new species are formed in an area, they will obviously influence the number of species present, and therefore genetics is also a historical factor to be considered.

The time factor appears to be of more importance than the other two historical

factors. A certain amount of time is required for organisms to occupy the slide, or in the case of "young" water (Steemann-Nielsen 1954), a period of time is necessary for pioneers to invade a water mass. Therefore, according to whether the organisms are benthonic or planktonic, the age of the substrate or of the medium would affect the number of species present. Time is a successional phenomenon as illustrated in the figures, and is important in succession in combination with other factors, as discussed below.

Proximity to the general optimum has perhaps the most important influence on the species variety of an area, inasmuch as whether or not species are able to live there is determined by this proximity. In attempting to define this, however, considerable difficulty is met because of the numerous factors that contribute to it. The general optimum may, however, be defined as the environmental conditions under which the majority of species on the earth live. General optimal conditions therefore should probably be looked for in the tropic marine environment, inasmuch as a larger number of species per habitat probably live under conditions there than anywhere else—but when the insects and terrestrial plants are considered perhaps the terrestrial environment more nearly approaches the general optimum than the aquatic. At any rate, the only way to measure it appears to be to determine the number of species that are able to live under its conditions.

Among the conditions which may be considered in a discussion of the general optimum are two chief types, abiotic and biotic. Abiotic factors which must be considered to influence species variety are numerous. Two might be used as examples, temperature and pH in their relations to the blue-green algae of the Yellowstone area (Vouk 1950). Vouk reported that at 10°C, 44 species of algae were found; at 35°, 90 species were found; and at 85°, only 6 were found. The optimal condition in regard to temperature for these algae in this area is therefore at about 35°C. How close this approximates the general optimum, however, is uncertain. Similarly, in regard to pH more than 90 species were able to live where the pH was about 8.3, whereas at 9.5 only 23 were able to exist, and at pH 3 only 2 species were found.

Biotic factors that influence species variety are also varied and probably equally as important as abiotic ones. Competition, for example, apparently has considerable influence on species numbers: these are less where competition is great than where it is negligible, as illustrated in Figures 1–10 of this report and discussed below. Predation or grazing presumably could eliminate one or more species from an area if great enough, and a lack of it would permit these species to exist. Harvey (1955: 23), for example, mentions that *Phaeocystis* is not eaten and hence would be represented in a floral list where grazing might eliminate other species.

When we consider the species variety of an area, it is necessary to delimit this area. It would be better to use the term habitat, inasmuch as in any one area many habitats may be present, each with its own characteristic species. If we compared two areas, say the surface water mass surrounding the Hawaiian Islands with one of the islands itself, then obviously the number of habitats present in each would greatly influence the species variety, the sparseness of habitats in the surface water mass showing a low species variety, and the numerous habitats of the land showing a high species variety. In comparing different areas as regards species variety, therefore, it appears essential to consider only one habitat at a time.

In each habitat there are a number of niches filled by various species; the number of niches apparently also would affect the species variety, so that this seemingly should also be considered. For example, if in one habitat, there are 5 species of herbivores and 3 carnivores, and in another, 5 herbivores and one carnivore, it would seem better to make the comparison by graphing herbivores against herbivores and carnivores against carnivores rather than species against species in total. I think, however, that where one trophic level is affected in species numbers, all other levels are probably also affected (in their turn—thus time is of importance at higher trophic levels as well

as at lower ones). For example, if 10 species of salps are found in an area with 5 carnivorous species of plankters and in another area only one species of salp is found, probably also fewer species of carnivores would be found inasmuch as both groups ultimately would be affected by the same conditions. Therefore, the niches of the various species in a habitat possibly need not be considered in a comparison, but only a species-individual curve.

An important factor in determining the species variety of an area, which combines both historical and general optimal factors, is productivity. Primary productivity is defined by E. P. Odum (1953: 78) as the rate at which energy is stored, by photosynthetic or chemosynthetic activity of producer organisms, in the form of organic substances that can be used as food. Consumer or secondary productivity is dependent on primary productivity, so that all parts of a trophic system are affected by the primary productivity. Productivity is therefore dependent on biogenic factors available to the producer organisms in a habitat: the energy source, light; water; materials in solution used in building these organic compounds, such as phosphates and nitrates; etc. In addition, productivity by its definition is dependent on time, a historical factor.

As regards effects on species variety, factors that affect productivity affect density of the organisms, which in turn affects the number of species in a habitat as shown in Figures 1–10. The high production station showed that the density became great in a short time, which was reflected in the large numbers and few species. The station with low productivity, however, showed only a slight but gradual increase in numbers with time although eventually numbers became dense enough to produce a species reduction. An important effect of the time factor, then, is that any species-individual curve reflects the stage of succession the community is in only at that moment—a period of time before or after a curve from the same place might show an entirely different picture (cf. Figs. 1 and 4, rich station, for example). The changes in species variety with time, however, depend basically on other factors than time itself, such as productivity.

Coactions and perhaps particularly competition are probably lesser in habitats where there are many species but few individuals present than where there are great numbers of a few species, as indicated in Figures 1—10. A new habitat, for example a microscope slide, becomes occupied gradually by all the species of an area that can get to it and are able to live on it. Even in a high production area, at first there are few individuals of these many species. As density increases, due both to outside additions and reproduction of individuals in the new habitat, the frequency of encounter increases gradually, and as a result, those species better adapted to the conditions of this new habitat become numerous at the expense of those less well adapted. In the case of a low production area, however, inasmuch as density remains low, the frequency of encounter also remains low, permitting relatively many species to coexist, presumably indefinitely if production is low enough. It therefore is reasonable to presume that where productivity is great competition is also great, and the number of species present is small with large numbers of individuals. Conversely, where productivity is low competition is probably proportionately low merely because of fewer contacts between organisms in the same amount of space, as there are fewer organisms present, and therefore the number of species should be proportionately large. Thus, the variety of species apparently depends on the frequency with which different species encounter one another (frequency of encounter evidently applies as well to sessile organisms as to vagile ones). If the number of individuals of all species present on a slide increased considerably but the species variety did not change, the slope of the species-individual curve would remain high although it would move to the right. If certain species were eliminated while others increased in numbers, the slope would bend toward the abscissa and away from the ordinate, as is the case only in the curves that are from slides near or in an apparent

climax state. The slopes determined from counts from the low production station remain high, nearer the ordinate, far longer than at the rich station. These appear to reflect in turn the amount of competition as a result of the differences in productivity.

The question now arises, is it necessary to count more than ten fields to get a representative curve? The changes that occur with succession are reflected in the slope of the curve which apparently is independent of sample size beyond a low minimum of counts. One slide was studied in which the slope was the same after ten fields were counted, as after seventy fields (9,944 individuals). Although this needs statistical study, this is apparently the rule, inasmuch as a number of slides were counted beyond ten fields (most often, twenty) and in all these counts, the slope remained the same. The slope, therefore, can be reported as species per cycle (increase in number of species for each cycle increase of individuals), a measure which appears to be independent of sample size.

It is concluded from this study that in any habitat no one factor alone determines the species variety, but always a combination of factors. It is obvious that time and productivity must work together to have effects on the trophic systems, and that other conditions affecting the organisms of the habitats must also be considered for valid use of comparisons of species variety between two habitats. Thus, the conclusion by Patrick *et al.* (1954) that pollution eliminates the more sensitive species from a habitat thereby reducing competition, and that in rivers not adversely affected by pollution conditions are favorable for many species and competition is great may be premature. Two Silver Springs slides were analyzed by the same technique they used, that of Preston (1948). These slides were 54 days old: one was from the high production area and the other from ¼ mile downstream from the boil in the main current. Both analyses gave curves that closely approximated Figure 4 in Patrick *et al.* (1954), the curve from a polluted stream. The greatest number of species per interval in these Silver Springs counts was 7 as opposed to their 16, which places these slides even more toward the polluted type of stream (Silver Springs is, of course, unpolluted). It would seem more correct to presume that pollution has at least two effects, the one to eliminate sensitive species, but inasmuch as biogenic substances are added by pollution, the pollution is probably also simultaneously increasing, rather than reducing, competition.

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Phosphorus Release from Bog Lake Muds[1]

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ABSTRACT

The paper reports the results of some laboratory investigations concerning the mud-water phosphorus relationship of some Northern Wisconsin and Upper Michigan bog lake muds as influenced by lime, acid, and mechanical agitation.

Calcium carbonate added to the water phase of mud-water systems reduced the amount of soluble phosphorus from 8.0 to 0.8 parts per billion. The lime formed a thin crust at the mud-water interface, while the original pH of the bottom material prevailed at a depth of one-fourth inch below the mud surface. Agitation of the mud cores by stirring resulted in complete lime penetration throughout a three-inch core.

Experimental apparatus in which it is possible to obtain a 12°C temperature differential for stratifying water is described.

Radioactive ordinary superphosphate fertilizer was placed at various depths below the mud surface, and the percentage as well as the amount of phosphorus released to the water was indicated to be very small with virtually no phosphorus released from depths greater than one-fourth inch below the mud surface. Agitation by stirring of the muds resulted in approximately twice the concentrations of soluble phosphorus in the water phase of the agitated systems as compared to the undisturbed systems. The most effective means of releasing fertilizer phosphorus placed one-fourth inch below the mud surface was found to be the acidification of previously limed mud-water systems.

The mechanism of phosphorus suppression by the addition of calcium compounds to mud water systems is suggested to be adsorption of phosphate ions onto the surface of the calcium particles in a similar manner as that described by Boischot *et al.*

Large quantities of phosphorus are consistently found deposited in lake muds, but often the quantities of soluble phosphorus found in the waters are very small. If a mechanism could be discovered to increase the release of the phosphorus from the bottom muds so that it could contribute to the production of algae, and hence fish, it would be a valuable contribution. This research reports the results of some laboratory investigations concerning the mud-water phosphorus relationship as influenced by lime, acid, and mechanical agitation.

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LITERATURE REVIEW

A number of investigators have reported on the mud-water relationships of phosphorus in lakes. Einsele (1936) found that an insoluble ferric phosphate is precipitated when ferrous iron and phosphate occur together in the hypolimnion of eutrophic lakes and oxygen is added and the reaction is alkaline. The excess iron is precipitated out as ferric hydroxide. When oxygen is lacking in the muds, iron is reduced from the ferric to the ferrous state and phosphorus is free to go into solution. Thus in small shallow lakes phosphorus in the hypolimnion is in a cycle consisting of precipitation during the period of circulation and solution during the period of stagnation.

Ohle (1935, 1938) and Einsele (1938) have pointed out the significance of colloidal gels as nutrient regulators in lakes. Precipitated ferric hydroxide gel suspended in water containing phosphate was found to

adsorb the phosphate onto the ferric hydroxide gel. The adsorbed phosphate was again brought into solution by washing the gel with phosphate-free water.

Gessner (1939) found that the addition of calcium carbonate to natural waters caused a removal of phosphorus from solution. Gessner observed an approximately linear relationship between the addition of calcium carbonate and the decline in phosphorus content. Gessner also claimed that the removal of bicarbonate from solution by plants under conditions of high calcium content leads to the deposition of calcium carbonate and a reduction in soluble phosphorus content of the water.

Mortimer (1941, 1942) recorded the events in the hypolimnion after the onset of stratification and noted the accumulation of various nutrients in the water. The accumulation of nutrients in the water coincides with the increases in solubility accompanying reduction at the mud surface. The autumn oxidation period was accompanied by precipitation of the nutrients from the water.

Hutchinson and Bowen (1947, 1950) using radioactive phosphorus in Linsley Pond, Connecticut, noted that on introduction practically the whole of the phosphorus enters the phytoplankton and is sedimented. These investigators also noted that phosphorus passes into the littoral vegetation and from such vegetation into the free water again. A phosphorus cycle was postulated whereby the phosphorus liberated from the muds and entering the illuminated layers of water is taken up by phytoplankton and later sedimented out as a fine rain of particulate matter consisting of partly dead plankton and feces of zooplankton. The resultant movement of phosphorus is believed to be horizontal into the free water as phosphate ions and vertically as seston.

Hayes *et al.* (1952) added radioactive phosphorus to a small unstratified lake in Nova Scotia. These investigators postulated an active exchange between the water phosphorus and participating phosphorus in the lake solids, which together make up a single system. They hold untenable the proposition that some enhancement of plant or animal growth takes place.

EXPERIMENTAL APPARATUS

Pyrex glass tubing in units four feet long and 100 mm in diameter was used as containers for the mud-water systems. The bottom end of each tube was sealed with a large rubber stopper fastened to the tube with electrical "Scotch" tape. Two-quart cylindrical ice cream containers were placed in each tube to serve as containers for the bottom muds. The tubes were mounted in a vertical position in an aquarium, and a 15-watt electric light bulb was fastened in the top of each tube to serve as a heating unit to produce thermal stratification.

Thermal gradients were applied to the systems to reduce the amount of turbulent and convectional diffusion. A 12°C temperature-difference between the water above the mud surface and the water at the top of the column was produced by circulating cold lake water in the aquarium and employing the electrical heating system.

EXPERIMENTAL PROCEDURE

Natural hypolimnetic mud was procured with an Ekman dredge from Hummingbird and Moccasin lakes. The pH of the muds in the dry state as determined by the Hellige-Truog method ranged from 5.2 to 5.5.

To measure the depth of lime penetration into the bottom mud and the soluble phosphorus content of the water above the mud the following procedure was used. Bottom mud from Moccasin Lake was placed in a four-liter beaker to an approximate depth of three inches. Three liters of phosphorus-free distilled water were placed over the bottom mud with a minimum of disturbance to the mud surface. Lime in the form of calcium carbonate was applied at the rate of 0, 250, and 500 pounds per acre to the surface of the water and allowed to settle for a period of six weeks. The water surfaces of the mud-water systems were exposed to the air but protected from dust. At the end of the settling period the water was removed with a minimum of disturbance to the mud surface. The bottom mud was air dried to a firm consistency after which it was divided

into a thin surface section and three one-inch depth sections. The pH of the muds was determined by the Hellige-Truog method and the pH of the water by the glass electrode method. The soluble phosphorus was determined by the development of the molybdenum-blue color according to the method of Truog and Meyer (1929).

To measure the depth of lime penetration and its effect upon the suppression or release of phosphorus in an agitated system the same procedure was followed as that described for the undisturbed system with the following exceptions. Calcium carbonate was applied at the rate of 5 tons per acre to the surface of the water in one container at the time of agitation and to the surface of the water in the second container 72 hours after agitation. The third container served as a control and was agitated but did not receive an application of calcium carbonate. Agitation consisted of vigorously stirring the entire mud-water system with a glass rod for a period of two minutes. The bottom mud used in this experiment was from Hummingbird Lake.

Experiments designed to measure the percentage of ordinary superphosphate fertilizer in the water at various levels above the mud surface as related to placement of the fertilizer at various depths beneath the mud surface were carried out using the glass tube systems already described. P^{32} in the form of ordinary superphosphate fertilizer was obtained from the Plant Industry Station at Beltsville, Maryland. The fertilizer analyzed 20.4 per cent P_2O_5 and had a specific activity of 0.15 millicuries per gram of P_2O_5. Specific amounts of P^{32} superphosphate fertilizer were placed on the surface of the mud and at depths of one-fourth, one-half, and one inch below the surface in the four experimental tubes. Natural hypolimnetic mud from Hummingbird Lake was used in all tubes. Each tube was then filled with seven liters of phosphorus-free distilled water and allowed to stand for a period of 15 days, after which the water was sampled in one-liter aliquots at heights of 3, 18, and 32 inches above the mud surface. The water samples were then analyzed for radioactive phosphorus content.

One-liter samples of water were evaporated to a volume of less than 100 ml on a hot plate, filtered through Whatman 42 filter paper, and made up to volume in a 100-ml volumetric flask. An aliquot of the solution such that it would give less than 300 mg of $MgNH_4PO_4 \cdot 6H_2O$ precipitate was taken, and the radioactive phosphorus along with any additional phosphorus present was precipitated as magnesium ammonium phosphate according to a procedure adapted from Kolthoff and Sandell (1947). The magnesium ammonium phosphate precipitate was collected on an aluminum filter ring and prepared for counting in the Geiger-Mueller counter according to the method proposed by MacKenzie and Dean (1948).

An experiment designed to obtain information pertaining to the relationship between the amounts of phosphorus released by the fertilizer placed at various depths beneath the mud surface and the amount of mud and fertilizer surface exposed to the water was set up in a similar manner to the previously described experiment with the following exception. After the phosphorus-free water was added to the tubes each mud-water system was agitated with a glass rod for a period of two minutes after which the systems were allowed to stand for 15 days. The agitation as in the previous experiments consisted of vigorous stirring.

The tube experiments were repeated a third time to investigate the release or suppression of fertilizer phosphorus in the bottom muds as effected by applications of lime and sulphuric acid to the water phase of the mud-water systems. In the third experiment the radioactive phosphate fertilizer was placed one-fourth inch below the mud surface in all four tubes. The tubes were then treated as follows: No. 1 served as a control; No. 2 was limed with calcium hydroxide at the rate of 160 pounds per acre, and after 15 days was acidified to pH 3.4 with sulphuric acid; No. 3 received an application of 80 pounds per acre of calcium hydroxide; and No. 4 was limed at the rate of 40 pounds per acre calcium hydroxide. The calcium hydroxide form of lime was added in preference to the calcium car-

bonate form because of the higher neutralizing value of the hydroxide form.

RESULTS

Applications of lime in the form of calcium carbonate to the surface water of undisturbed mud-water systems formed thin crusts of lime at the mud-water interface. The data presented in Table 1 show the increased pH value in the mud surface layer. At the 500-pound-per-acre level of calcium carbonate the surface crust had an alkaline pH value, while the pH values of the deeper layers remained acidic.

The amount of phosphorus (8.0 parts per billion) released by the mud and present as soluble phosphorus in the water phase of the control system was of the magnitude found by Juday and Birge (1931) in northeastern Wisconsin lakes. Calcium carbonate added to the water phase of the mud-water systems reduced the amount of soluble phosphorus in the water to a trace—0.5 and 0.8 parts per billion.

Agitation or stirring of the mud-water systems following applications of calcium carbonate resulted in penetration of lime throughout the three-inch core of mud, as shown in Table 2. There was no apparent difference in the depth of lime penetration if the lime was applied directly before agitation or 72 hours later. This lack of difference can possibly be attributed to the slow rate of sedimentation following the vigorous stirring procedure. Approximately the same concentrations of soluble phosphorus were present in the water of the control and experimental systems for both the unagitated and agitated procedures (compare Tables 1 and 2).

The percentage as well as the amount of phosphorus released to the water from radioactive superphosphate fertilizer placed at various depths below the mud surface in an undisturbed mud-water system was indicated to be very small, as shown by the data presented in Table 3 and as previously reported by Hayes *et al.* (1952) in their studies of undisturbed cores taken with a Jenkins sampler. There was virtually no release of phosphorus from fertilizer placed at depths greater than one-fourth inch below the mud surface. There was a higher percentage of soluble phosphorus contained in the water samples taken near the mud surface than in water samples taken at greater distances above the mud surface. The radiophosphorus placed one-half inch below the mud surface showed only a very slight tendency to diffuse into the water, while the radiophosphorus placed at the one inch depth did not diffuse into the water at all. The concentrations of soluble phospho-

TABLE 1. *The pH values of bottom mud from Moccasin Lake at various depths below the mud-water surface, and the water soluble phosphorus content of limed and unlimed undisturbed systems in a laboratory experiment*

Treatment (lbs. $CaCO_3$ per acre)	Bottom mud			Water		
	Depth (inches)	pH		pH		Soluble phosphorus (parts per billion)
		Before treatment	6 weeks after treatment	Before treatment	6 weeks after treatment	
Control	surface	5.5	5.5	5.65	5.65	8.0
	1/4	5.5	5.5			
	1–2	5.5	5.5			
	2–3	5.5	5.5			
250	surface	5.5	6.8	5.65	6.80	0.5
	1/4	5.5	5.5			
	1–2	5.5	5.5			
	2–3	5.5	5.5			
500	surface	5.5	7.5	5.65	7.05	0.8
	1/4	5.5	6.0			
	1–2	5.5	5.5			
	2–3	5.5	5.5			

TABLE 2. *The pH values of bottom mud from Hummingbird Lake at various depths below the mud-water surface, and the water soluble phosphorus content of limed and unlimed agitated systems in a laboratory experiment*

Treatment (5 tons $CaCO_3$ per acre)	Bottom mud			Water		
	Depth (inches)	pH		pH		Soluble phosphorus (parts per billion)
		Before treatment	6 weeks after treatment	Before treatment	6 weeks after treatment	
Control	surface	5.3	5.3	5.65	5.55	6.0
	1–2	5.3	5.3			
	2–3	5.3	5.3			
Added at time of agitation	surface	5.3	8.3	5.65	7.52	0.3
	1–2	5.3	8.3			
	2–3	5.3	8.3			
Added 72 hrs. after agitation	surface	5.3	8.3	5.65	7.63	0.4
	1–2	5.3	8.3			
	2–3	5.3	8.3			

TABLE 3. *Diffusion and convection of P^{32} superphosphate fertilizer in an undisturbed mud-water system*

Water samples collected after 15 days.

Placement of fertilizer below mud surface (inches)	Fertilizer added (grams)	Relative specific activity of fertilizer (counts per second)	Height of water sample above mud surface (inches)	Sample (zero count per second)	Per cent uptake by water
surface	2.0052	130,739	32	1539	1.177
			18	1333	1.020
			3	1838	1.406
0.25	2.0193	131,658	32	579	0.440
			18	667	0.506
			3	1392	1.058
0.50	1.8385	119,870	32	76	0.063
			18	66	0.055
			3	177	0.148
1.00	1.9963	130,159	32	0	0.000
			18	0	0.000
			3	0	0.000

Note: A thermal gradient of 8°C was established and maintained between the mud surface and a point 12 inches above the mud surface.

TABLE 4. *Diffusion and convection of P^{32} superphosphate fertilized in an agitated mud-water system*

Water samples collected after 15 days.

Placement of fertilizer below mud surface (inches)	Fertilizer added (grams)	Relative specific activity of fertilizer (counts per second)	Height of water sample above mud surface (inches)	Sample (zero count per second)	Per cent uptake by water
surface	1.9883	129,637	32	2771	2.137
			18	2805	2.164
			3	3065	2.364
0.25	2.2174	144,574	32	2107	1.458
			18	2144	1.483
			3	2331	1.612
0.50	1.9944	130,035	32	1891	1.454
			18	1828	1.406
			3	2025	1.557
1.00	1.9545	127,433	32	855	0.671
			18	932	0.732
			3	875	0.687

rus in the water phase of each treatment based upon the average of the three water samples taken from each treatment were 2.1, 1.2, 0.1, and 0.0 parts per billion arranged in order of increasing depth of fertilizer placement below the mud surface.

Agitation or stirring of the bottom muds containing radioactive ordinary superphosphate fertilizer at the same depth placements as in the undisturbed systems resulted in approximately twice the concentrations of soluble phosphorus in the water phases of the agitated mud-water systems, as shown by a comparison of Tables 3 and 4. The concentrations of soluble phosphorus in the water phase of each treatment based upon the average of the three water samples taken from each treatment were 3.9, 2.9, 2.7, and 1.2 parts per billion arranged in order of increasing depth of fertilizer placement below the mud surface.

Acidification of previously limed mud-water systems proved to be the most effective means of releasing fertilizer phosphorus "planted" one-fourth inch below the mud surface. As shown in Table 5 the acidification of pH 3.4 with sulphuric acid of the water phase of a mud-water system that had previously been limed with calcium hydroxide at the rate of 160 pounds per acre caused a greater release of phosphorus to the water than the control or limed systems. The percentage of phosphorus released from mud to water decreased as the rate of liming increased.

TABLE 5. *The effect of liming and acidification upon the diffusion and convection of P^{32} superphosphate fertilizer in a mud-water system*

Treatment	Fertilizer added (grams)	Relative specific activity of fertilizer (counts per second)	Height of water sample above mud surface (inches)	Sample (zero count per second)	Per cent uptake by water
Control	1.1909	77,595	32	485	0.625
			18	555	0.715
			3	573	0.739
160 lbs. $Ca(OH)_2$ per acre for 15 days; acidified to pH 3.4 for 15 days	1.6374	106,758	32	1102	1.033
			18	1274	1.193
			3	1192	1.117
80 lbs. $Ca(OH)_2$ per acre for 30 days	1.0143	66,132	32	39	0.059
			18	31	0.047
			3	48	0.073
40 lbs. $Ca(OH)_2$ per acre for 30 days	1.1128	72,555	32	104	0.143
			18	122	0.168
			3	155	0.214

DISCUSSION

Located near the Upper Michigan-Wisconsin boundary in Vilas County, Wisconsin, and Gogebic County, Michigan, are a

large number of soft-water bog lakes. These lakes are dystrophic in nature, low in nutrient content as well as in soluble and total iron content, and they have a high content of organic matter which lends a dark color to the water.

Lime has been added to a number of these lakes in an effort to increase the depth of light penetration into the water. In addition the lime prevents summer-kill due to high temperatures by providing oxygen in the cooler water of the thermocline, and prevents winter-kill in marginal cases by reducing the amount of oxygen consuming colloidal organic matter (Hasler *et al.* 1951).

In pursuing the above management procedure further, changing the reactions of the water and bottom muds by the addition of lime or some other chemical might have the effect of liberating plant nutrients such as phosphorus into the water. This would ultimately increase the growth of phytoplankton and zooplankton thus increasing the fish carrying capacity of the lakes.

Phosphorus occurs in soils in both the organic and inorganic form. There has been evidence presented that some mineralization of organic phosphorus in the soil occurs (Schollenberger 1920, Robinson 1937), and that this phosphorus is of value in the nutrition of higher plants only when it is changed to the inorganic form (Eid, Black, and Kempthorne 1951, 1953). In the case of lower plants Chu (1946) has reported that the growth of *Phaeocystis Pouchetii* was a little better and lasted longer when phytin was supplied to natural sea water as a source of phosphorus than when orthophosphate was supplied.

The depressing effect of calcium upon the solubilities of the various phosphates has been pointed out by Larson (1935), Gaarder (1930), McGeorge and Breazeale (1931), McGeorge (1939), and Gessner (1939). The mechanism of this reaction has been described by McGeorge and Breazeale (1931) as the formation of a new compound of lower solubility such as hydroxylapatite. Another possible mechanism of this reaction has been described by Boischot *et al.* (1950), who stated that a new compound is not necessarily formed, but instead the phosphate ions are adsorbed on the surface of the calcium carbonate crystals as an initial reaction. Cole *et al.* (1953) confirmed this theory and advanced the idea of monolayer adsorption of phosphate ions by calcium particles.

In an alkaline or neutral medium calcium phosphates are virtually insoluble; however, in soils the calcium phosphate compounds represent an easily available form of phosphorus for plant nutrition because of the solubility of the phosphorus compounds in dilute acids of a strength corresponding to that produced by plant roots.

Based on the previously stated theories it is therefore conceivable that when calcium in the form of lime is added to the surface water it adsorbs the phosphate ions onto the calcium particles as they fall through the water. The portion of the calcium particles that settle into the bottom material and upon the mud surface is believed to act in two ways. The calcium particles that settle on the mud surface might in effect form a seal that prevents or greatly restricts the diffusion of any phosphate ions released by the muds to the water phase of the system. It is also suggested that a portion of the calcium particles entering the mud phase of the system converts some of the iron and aluminum held phosphorus compounds to calcium phosphates. Subsequent acidification of the water phase of the mud-water system releases some of the calcium held phosphorus to the water in the same manner as plant root acids act upon soils. Likewise rooted aquatics growing in the littoral zone would have more phosphorus available for their nutrition from calcium phosphates than from iron and aluminum phosphates.

The results obtained by the use of radioactive phosphorus in agitated or stirred muds suggests the possibility of raking or harrowing the muds of small bays or ponds as a method of releasing more phosphorus into the water. Hayes *et al.* (1952) suggest that the thickness of the mud layer participating in the exchange is approximately one millimeter. Therefore it would seem feasible that the release of phosphorus from mud is a function of the amount of surface exposed to water rather than thickness of the mud layer. Thus by harrowing, discing,

or raking the bottom muds the amount of mud surface exposed to water and therefore able to participate in the exchange process would be greatly increased.

It should be pointed out that Ohle (1935, 1937) measured considerable amounts of phosphorus leeching out of alkalized bog lake muds. The lack of acid production by bacterial action might be attributed to the low bacterial population supported by the impoverished sandy soils that predominate in the region where these lakes occur. It should also be noted that leaching is a process where liquids are actively moving through a solid medium and is quite unlikely to occur in lakes while diffusion is one of the established processes by which nutrients are released from mud to water in mud-water systems.

SUMMARY

1. The results of some laboratory investigations concerning the mud-water phosphorus relationship as influenced by lime, acid, and mechanical agitation are reported.

2. Experimental apparatus in which it is possible to obtain a 12°C temperature gradient in water is described.

3. Applications of lime in the form of calcium carbonate to the surface water of undisturbed mud-water systems formed thin crusts of lime at the mud-water interface, while the original pH of the bottom material prevailed at a depth of one-fourth inch below the mud surface.

4. Calcium carbonate added to the water phase of mud-water systems reduced the amount of soluble phosphorus from 8.0 to 0.8 parts per billion.

5. Agitation of mud-water systems following applications of lime resulted in complete lime penetration throughout a three inch mud core.

6. The percentage as well as the amount of phosphorus released to the water from radioactive ordinary superphosphate fertilizer placed at various depths below the mud surface in an undisturbed mud-water system was indicated to be very small, with virtually no phosphorus released from depths greather than one-fourth inch.

7. Agitation of the bottom muds containing radioactive ordinary superphosphate fertilizer at the same depth placements as in the undisturbed systems resulted in approximately twice the concentrations of soluble phosphorus in the water phases of the agitated systems as compared to the undisturbed systems.

8. Acidification of previously limed mud-water systems proved to be the most effective means of releasing fertilizer phosphorus placed one-fourth inch below the mud surface.

9. The percentage of phosphorus released from mud to water decreased as the rate of liming increased.

10. The mechanism of phosphorus suppression by the addition of calcium compounds to mud-water systems is suggested to be adsorption of phosphate ions onto the surface of the calcium particles in a manner similar to that described by Boischot *et al.*

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Bathypelagic Coelenterates[1]

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ABSTRACT

Four different kinds of hydrozoan medusae, two of scyphozoans, and four of siphonophores are recorded from three basins of southern California, largely in depths greater than 4000 feet. The records are based on photographs made with a special underwater camera which is described. These coelenterates show specific distributional patterns which appear to reflect not only limited tolerances to temperatures, but also preferences for certain foods either near the sea floor or in the sound-scattering layers.

INTRODUCTION

Many of the animals that live at great depths in the ocean are soft and gelatinous. When caught in trawl nets they break up and wash between the cords. Some of them live just above the bottom where trawling is hazardous to equipment. For these reasons the deep-water forms are but little known from specimens. During the course of a program of underwater photography off southern California by the Allan Hancock Foundation (Emery 1952) many pictures have shown bathypelagic (deep water) coelenterates of several kinds. They were made with a 70-mm camera housed in a steel sphere 39 inches in diameter with walls 1½ inches thick and having one quartz window for the camera and another for a stroboscopic light (Fig. 1). The camera shutter was synchronized with the light, which flashed at 30-second intervals. Enough film was carried in the camera to allow the making of 325 photographs during a span of 2½ hours. Ordinarily, the equipment was started at the surface and allowed to operate while being lowered, while held on or just above the bottom, and while being hoisted back to the surface. On deck, records were kept at one-minute intervals of the amount of cable overside. These records permitted the identification of the depth at which each picture was made.

Twenty-two useful lowerings of the device, called the benthograph, were made between 22 May 1950 and 10 July 1952, when it was lost at a depth of 2440 feet. About 5000 individual photographs were taken. Many of the lowerings were on the bottom or side slopes of three deep basins (Fig. 2). Color film, used in five lowerings, showed but few organisms in the water column, possibly because of low sensitivity of the film. In one color film and in all black-and-white films many objects may be seen in the pictures of the water column. Most of them are small, indistinct, and at depths shallower than 2000 feet; they are probably related to the sound-scattering layer or "false bottom" (Emery 1952). Larger and more clearly defined are the animals that were photographed at greater depth. Nearly all of the identified deep forms are coelenterates, including hydromedusans, scyphozoans, and siphonophores. Only a few fishes and one prawn were noted. Use of nets in upper and middle water levels has demonstrated the presence of many macroplanktonic (more than ½ inch across) animals. Some so taken have been ctenophores (*Pleurobrachia*, *Beroë*), tunicates (especially *Pyrosoma* and *Oikopleura*), chaetognaths or arrow-worms, larger crustaceans, and others. These have not been observed on photographs.

We wish to extend special thanks to Captain Allan Hancock for his continued interest and support.

HYDROZOAN MEDUSAE

Hydrozoan medusae in shallow water are best known for their bottom or polyp stages as feathery or branched colonial growths

[1] Contribution of Allan Hancock Foundation No. 179.

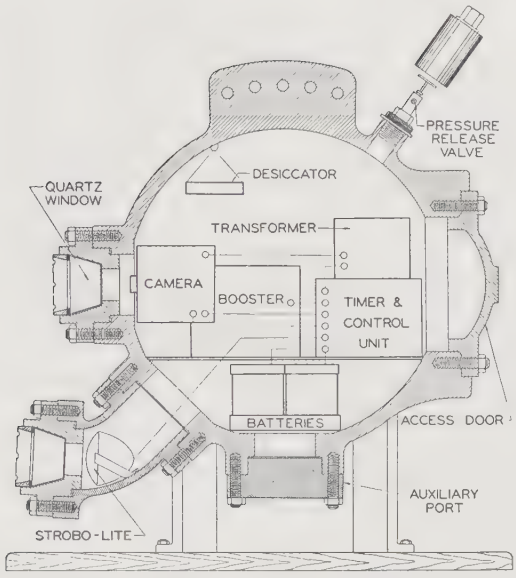

FIG. 1. Cross-section of benthograph showing construction details and equipment used for photography in the water.

called hydroids attached to rocks or other solid objects. This asexual stage, by budding, gives rise to sexual dioecious medusae which may measure only a fraction to several inches across the disk. For most kinds the medusa stage is small or unknown. For other kinds the medusa stage may be known and its hydranth stage unknown. One of the best known in California is *Polyorchis*, which attains a diameter of 2½ to 3 inches (Skogsberg 1948) and its tentacles number 40 to 150. Another much smaller medusa, *Monobrachium parasitum* Mereschkowsky, measuring ¼ to ½ inch across the disk, has been found (unpublished data) in considerable abundance in the shallower parts of Santa Monica Bay, California, adhering to its hydranth stage which is commensal with *Axionopsis* sp. (a bivalve mollusk). Others, of larger size, are trachyline medusae of various kinds; some have been recorded between the surface and 1650 feet (vertical hauls) in Monterey Bay (Bigelow and Leslie 1930). They differ from those reported below.

The deep water hydrozoan medusae appear uniformly white or somewhat translucent and without a pigment pattern. Their disks are circular and of considerable size, approximately 3½ to 8 inches in diameter. Tentacles are inserted subterminally and number from 23 to 32. According to the photographs the umbrella or bell has an entire, not scalloped, margin, and the mouth is at the end of a longer or shorter manubrium or neck. Another fundamental character, whether the gonads are on the radial canals as in the Trachymedusae, or in the floor of the gastric cavity as in the Narcomedusae, cannot be determined from examination of the photographic film alone. Specific identification must await collection of specimens, but for the present they are considered to be trachyline Trachymedusae. Four kinds have been noted.

The most abundant kind of trachyline medusa (Plate 1) is characterized by a long manubrium, the disk is an estimated 3½ to 4 inches in diameter, and the 23 to 32 tentacles are 2½ to 6 inches long, varying with size of the individual. This species has its greatest concentration in San Nicolas Basin, but was also observed in Catalina Basin. Altogether 79 individuals were counted. Its typical horizon a short distance above the bottom and its long manubrium suggest that it feeds on animals existing near, on, or in the sediments of the sea floor.

A second kind of trachyline medusa (Plate 2, A) is characterized by a very flat umbrella, a short manubrium, about 32 tentacles, and the margin of the bell is entire. The disk, probably circular, has an estimated diameter of 5½ inches and the length of the tentacles is about 6¾ inches. Only one individual was seen. Its presence in the sound-scattering layer of Catalina Basin suggests that it may prey on the organisms associated with this layer.

A third, perhaps much smaller kind of medusa (Plate 2, B) has a flattened umbrella. It also differs from the others in that the tentacles appear to form two series, one directed stiffly out at the sides, the other at right angles to the oral side. This medusa was observed only once.

The fourth kind of medusa has a tangled mesh of long, slender, distally enlarged tentacles (Plate 2, C). It is presumed to be

PLATES 1–4

PLATE 1. Trachyline medusae—most abundant form.

A. Station 2087 at 5800 feet.
B. Station 2087 at 5760 feet.
C. Station 2087 at 5765 feet.
D. Station 2083 at 5589 feet. Part of a swarm of at least 14.

PLATE 2. Trachyline medusae—rare forms and scyphozoan medusa.

A. Station 2099 at 1225 feet. Trachyline medusa seen in the sound-scattering layer.
B. Station 2083 at 3990 feet. Another kind of trachyline medusa.
C. Station 2102 at 1045 feet. *Gonionemus*-like medusa.
D. Station 2111 at 4360 feet. Scyphozoan medusa.

PLATE 3. Siphonophores and Scyphozoan.

A. Station 2097 at 1549 feet. Part of axon of an abylid siphonophore. Note successive light and dark areas.
B. Station 2097 at 1549 feet. Abylid siphonophore with part of tail cut off (turned 90° to the right).
C. Station 2096 at 2806 feet. Abylid siphonophore (turned 90° to the right).
D. Station 2083 at 380 feet. Abylid siphonophore with zig-zag tail.
E. Station 2096 at 2916 feet. Abylid siphonophore and campanulate scyphozoan.

PLATE 4. Bathyphysid siphonophores.

A. Station 2096 at 2915 feet.
B. Station 2100 at 2060 feet (turned 90° to the right).
C. Station 2100 at 2080 feet. Part of an axon.

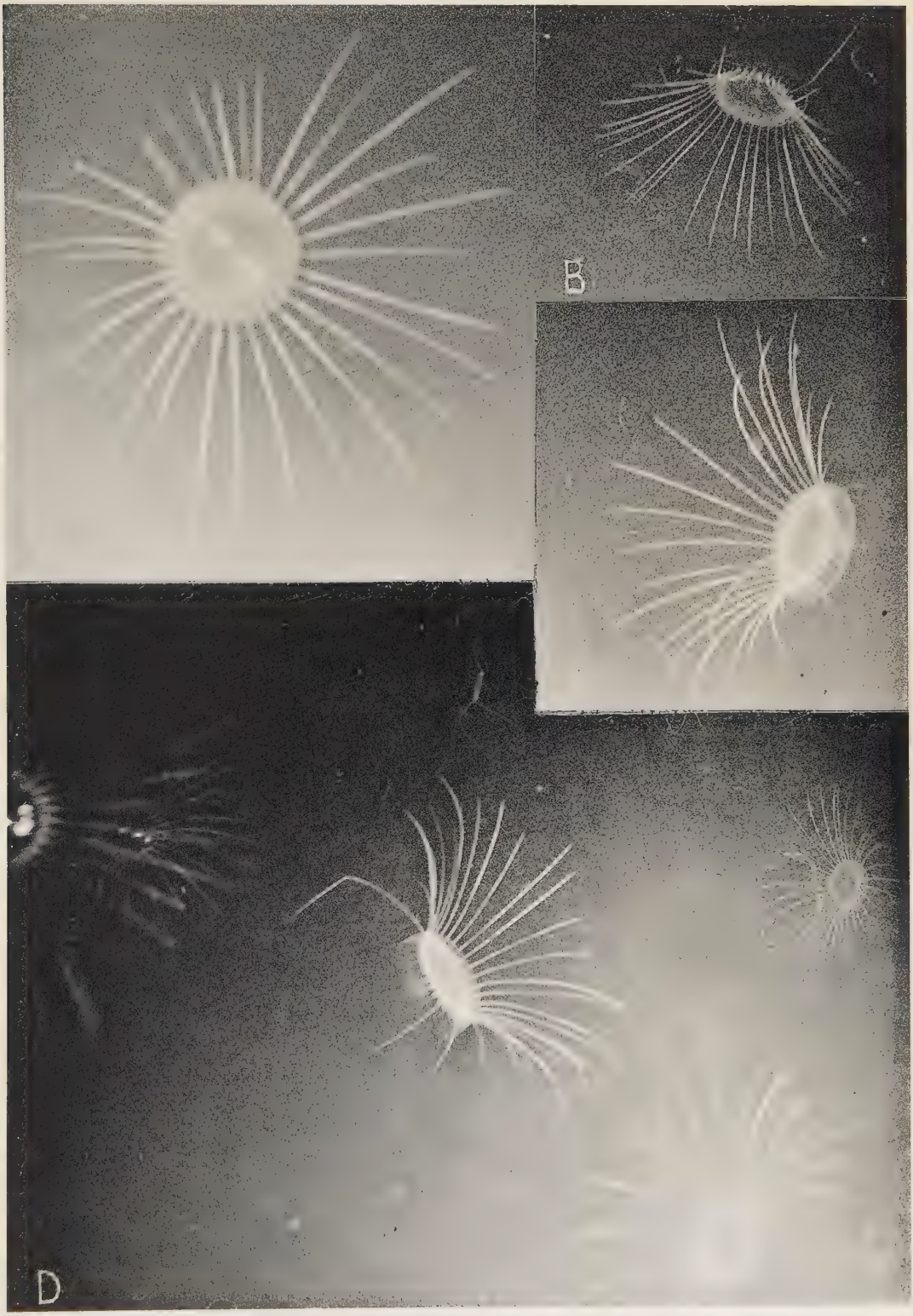

PLATE 1

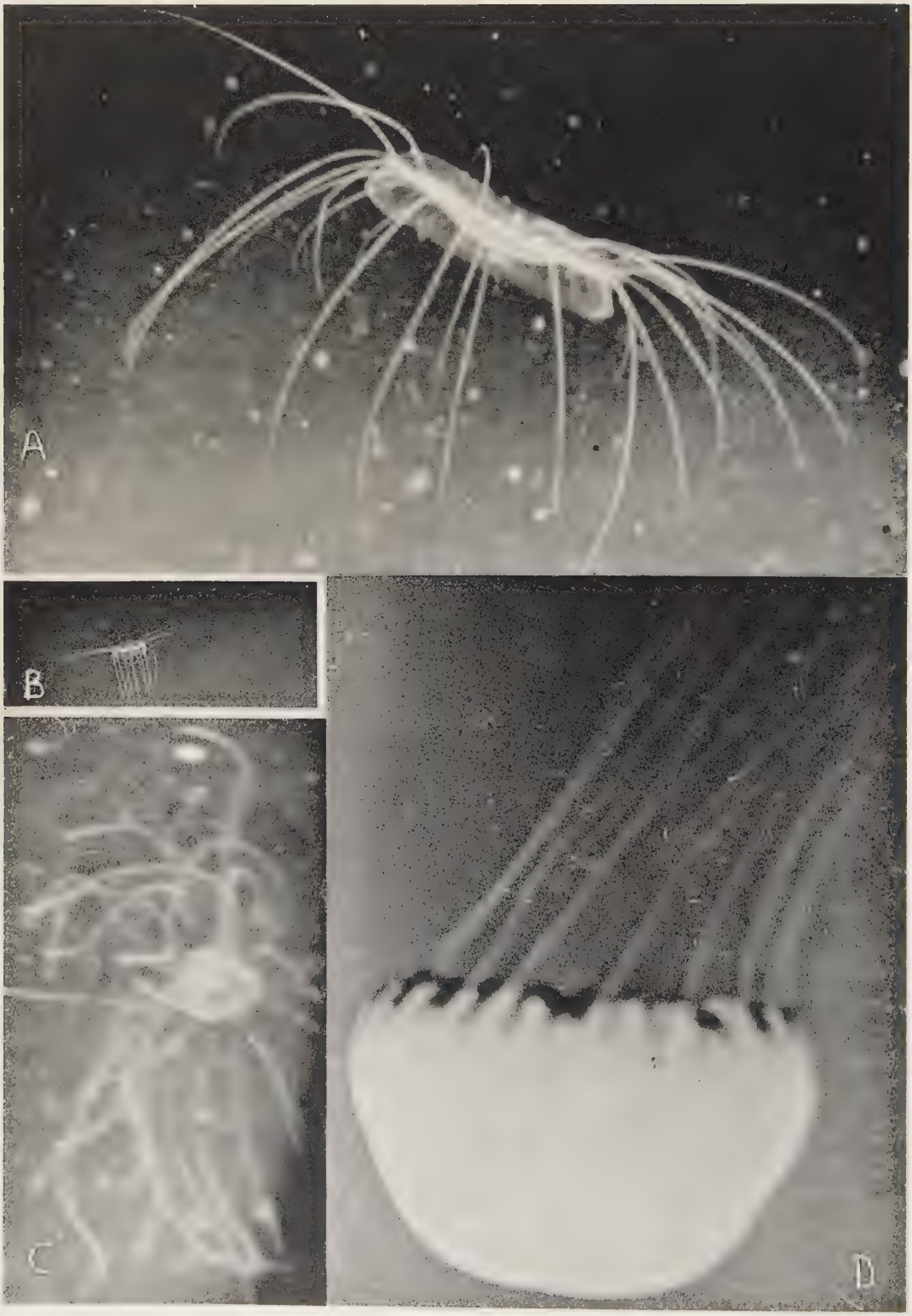

PLATE 2

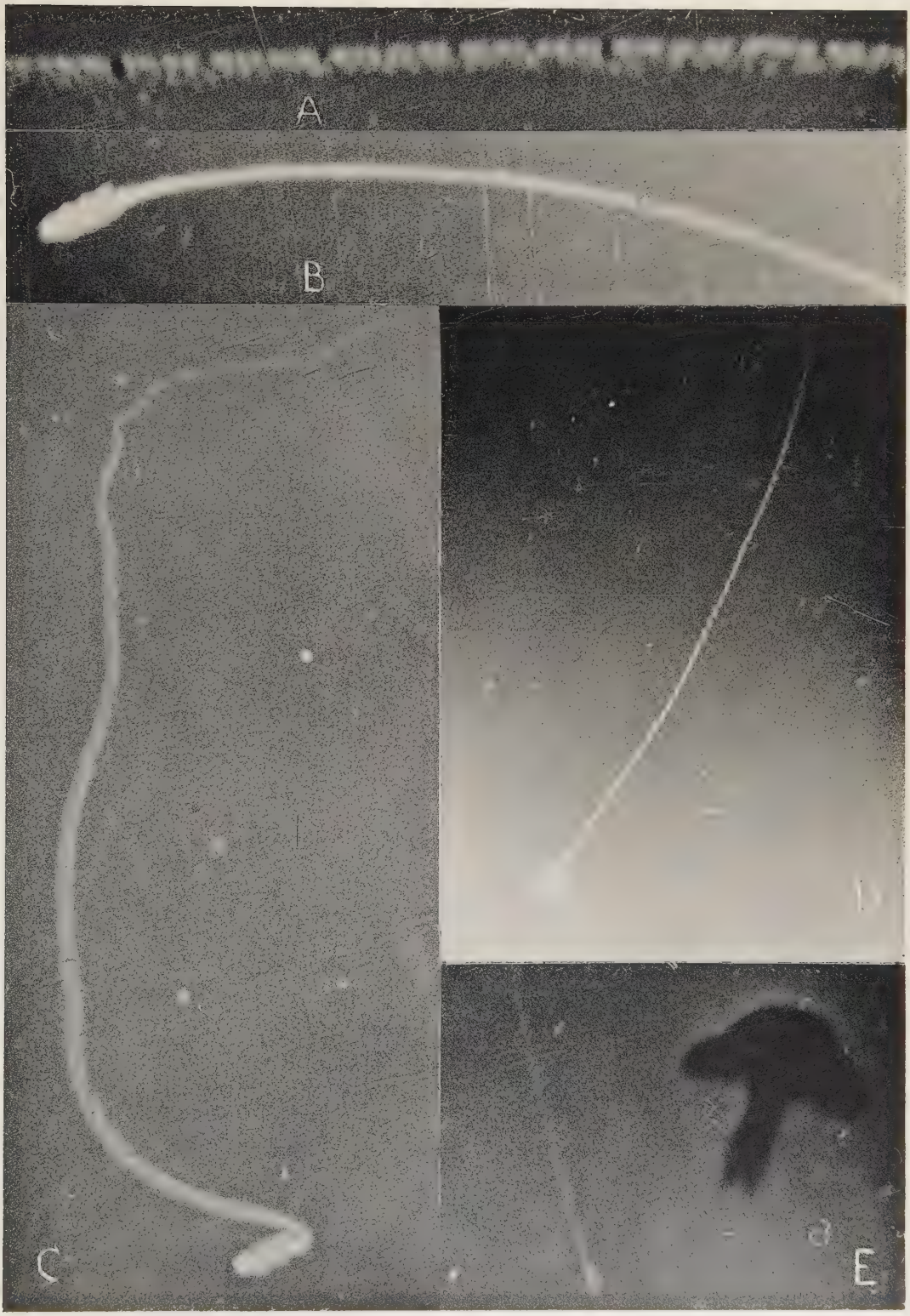

Plate 3

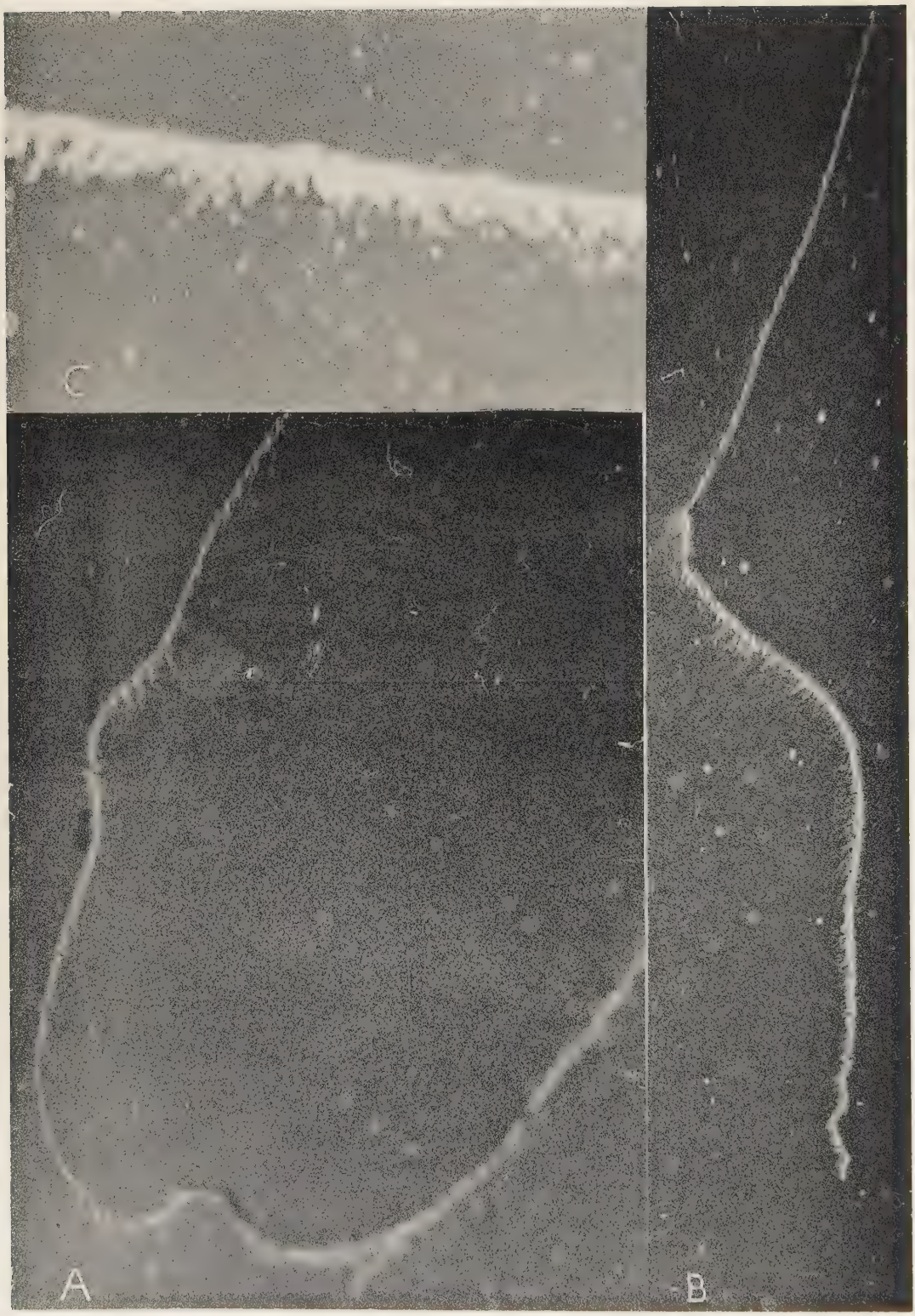

PLATE 4

a trachyline medusa having affinities with *Gonionemus*, in the family Olindiidae; these are characterized by hollow tentacles, and adhesive disks on some or all tentacles, adapted to clinging to algae. One such from California is *Vallentinia adherens* Hyman (1947), described from algal associations in shallow water. Another related species from the warmer areas of eastern United States is *Olindias phosphorica tenuis* Fewkes, for which the interesting nocturnal habits have been described by Breder (1956) who reported the medusae actively predaceous on fishes at night and resting in algal strands during the day. The medusa was observed on the film only once, near the bottom on the side slope of San Pedro Basin.

SCYPHOZOA

Scyphozoan medusae, or jelly-fishes, differ from hydrozoan medusae in several ways. Usually they are larger, some attaining gigantic proportions. The bell is more opaque and lacks a shelf or velum along its inner edge. The mouth is commonly surrounded by frilled lobes. They are frequently encountered in shallow or moderate depths. Sometimes cast ashore is the beautiful white and purple radially striped *Pelagia cyanella* Péron and Leseuer, which may be 12 inches across and has eight slender tentacles and four oral lappets. The dark brown *Chrysora gilberti* Kishinouyi may grow to be nearly as large; it has 24 tentacles, an umbrella flatter than that of *Pelagia*, and four oral tentacles that are much frilled at the margins. The white sea-jelly, *Aurelia aurita* Lamarck, is more delicate; it lacks long marginal tentacles but has a close fringe of many very short ones. The large sea-blubber, *Cyanea capillata* Eschscholtz, may measure 6½ feet across the disk and the tentacles may extend 60 feet; in life it is bright yellow or orange. The beautiful Prussian blue jelly-fish in shallow waters of California is *Stomopholus melaegris* Agassiz.

All of the forms described above occur at moderate or shallow depths in waters of comparatively high temperature. They are considered cosmopolitan in distribution with temperature the limiting factor. Others in deeper colder water are shown in photographs from Catalina and San Pedro Basins. One near the bottom of Catalina Basin (Plate 2, D) may be about 12 inches across; its long slender streaming marginal tentacles are seen in swimming position, and the bell is directed downward. Another kind of scyphozoan medusa near the bottom of San Pedro Basin (Plate 3, E) has long frilled oral lappets and a campanulate bell. This is associated with organisms in the sound-scattering layer and with siphonophores.

SIPHONOPHORES

The best known representatives of siphonophores in California are those inhabiting the shallow layers of the sea. The strand of windswept beaches is sometimes strewn with countless thousands of small epiplanktonic, rafted Blue-sail, *Velella lata* Chamisso and Eysenhardt, with individuals 3 to 4 inches long. Tropical areas have the more conspicuous and formidable Portuguese-man-of-war, *Physalia pelagica* Bosc. Its enormous brilliantly colored floating pneumatophore may be 12 inches long, and from its lower surface the varied array of tentacles may extend 20 to 45 feet. Both of these are surface forms that can exist only if their floats are maintained upright above the surface of the water. Each is a colony of highly specialized individuals named for their function and attached at nodes along a stem or axis that may be several yards long. Nectophores, or modified bell-like individuals at the forward end, jet-propel the colony through the water. In the Physophorida, to which *Velella* and *Physalia* belong, the float is called a pneumatophore.

Deep water siphonophores also are colonies of hydrozoan coelenterates, characterized by consisting of different kinds of individuals: gastrozooids or siphons ingest food, gonozooids are reproductive and dioecious (sexes separate), dactylozooids or feelers are sensory detecting, and the bell or float serves to propel the colony through the water. A gastrozooid is provided with a single hollow, long, contractile tentacle with lateral branches or tentilla, each of which

ends in a knob or coil of stinging cells or nematocysts. The swimming bell is surmounted by a thick gelatinous bract of various shapes. When these seried groups of individuals are still attached to a colony, they are collectively called a cormidium, each differing in age so that the distalmost from the nectophore is the oldest one. When they break away from the colony they are called eudoxomes and it is as such that they are most frequently taken in nets. Since the entire colony is very fragile and gelatinous, it cannot be taken in good condition by ordinary collecting methods.

The nectophore, from which most generic and specific descriptions (Davis 1955: 209) have had to be made, is a complex gelatinous sack shaped like a prism, a helmet, or a flattened truncate or rounded bell and sometimes of minute proportions compared with the size of the colony. Its outer surface consists of a series of facets separated from one another by serrated or smooth ridges. The individual facets are named and lettered with reference to their position about the opening of the hydroecial cavity. They vary further according to the number of their sides and whether they are concave, convex, or straight; their ridges may be simple or divided, and the facets may meet one another at acute to blunt angles. Such detailed characters have provided the base for both specific and subfamilial ranks. The names Monophysid and Diphysid have been used to designate the numbers of distal nectophores, whether single or multiple, but since the bells are subject to loss or replacement, and may number more than four, the designations are inapt. Individual nectophores have been described with sizes ranging from ⅛ to ¼ inch long and 1/16 to ⅛ inch wide (Lens and Riemsdijk 1908). Fragments of these are sometimes taken in nets or trawls or cast ashore during storms. When so taken they are usually injured or disrupted. From these fragments it is difficult to reconstruct entire colonies, or to estimate the general form or size of the colony. Underwater photographs can provide more accurate records.

At least four different kinds of siphonophores have appeared on photographs made in San Pedro Basin, and with less frequency in Catalina Basin, in depths ranging from 170 to 3475 feet below the surface. They are presumed to be calycophorids (see Hyman 1940 for systematic discussion) and may belong to genera in the subfamily ABYLINAE Lens and Riemsdijk, genera *Abyla*, *Diphyes*, and *Muggiaea*, or related kinds. The subfamily is characterized for having one or more nectophores in superimposed series when more than single. The most abundant kind (Plate 3, B, C) may be an abylid siphonophore. It is represented by 35 individuals in 26 pictures from five stations, all in San Pedro Basin except one in Catalina Basin, and mainly in deep water near the bottom. This kind appeared singly in 19 photographs, twice in 5 photographs, and three times in 2 photographs. The greatest numbers were in San Pedro Basin at depths of 1568 to 2915 feet, a short distance above the sea floor. Some of the films show individuals with as many as four nectophores in superimposed series (Plate 3, B), together estimated at 2 inches long; they are followed by a long more slender tail or axon estimated at more than 3 feet long. The axon carries the polymorphic individuals in straight linear series, resembling a string of beads, in which a dark one is interspersed at nearly regular intervals (Plate 3, A). These dark spots may represent the siphons or another kind of member of the colony.

Another kind of siphonophore has a single prismatic nectophore and a long slender zig-zag tail or axon (Plate 3, D). It was photographed only once, from San Nicolas Basin.

A third kind of siphonophore was observed three times but never in sharp focus. It has a single sharply conical or pyramidal nectophore, resembling that of species of *Diphyes* or *Galeolaria*. It occurs at intermediate depths in San Nicolas and Catalina Basins.

An altogether different kind of siphonophore, with long pendanted individuals shown on some photographs, is presumed to be a bathyphysid siphonophore. Members of this group are characterized by a bell that is small for the size of the colony.

The axon is long and provided with irregularly prolonged individuals suspended at various intervals (Lens and Riemsdijk 1908). One of the largest is *Pterophysa grandis* Fewkes, which reaches a known length of 11½ feet and is recorded from depths as great as 4608 feet. Photographs made in deep water show large ropey strands, perhaps representing members of this group (Plate 4). They are recorded singly in ten photographs at four different stations in San Pedro and Catalina Basins and at depths of 1375 to 2915 feet.

DISTRIBUTION AND SIGNIFICANCE

The distribution of bathypelagic coelenterates in the basins, as judged from the photographs, shows a segregation or preference for different basins by the various forms. All except two of 82 individual trachyline medusae occur below the sills of two basins—San Nicolas and Catalina (Figs. 2 and 3). These waters are the coldest of those studied by the camera, 3.7° and 4.0°C (Emery 1954). In contrast, nearly all of the siphonophores are from the bottom of the warmer (5.1°C) San Pedro Basin or from the even warmer side slopes of San Pedro and Catalina Basins. Thus, apparently the trachyline medusae and the siphonophores have different temperature preferences. Another control, considered by us to be less effective than temperature, is that of oxygen content of bottom waters. This averages 0.60, 0.45, and 0.25 ml/L for the San Nicolas, Catalina, and San Pedro Basins, respectively (Rittenberg *et al.* 1955).

The characteristic common to the trachyline medusae, scyphozoans, and siphonophores is the preference for waters just above the bottom. Of 138 individuals in the photographs, 112 occurred within 300 feet of the bottom. This suggests that they feed on animals on or in the bottom sediments. The bottoms of both Catalina and San Nicolas Basins have been found (unpublished data) to support a diversified population of metazoan invertebrate animals, but in contrast the floor of San Pedro Basin is nearly barren (Hartman 1955a). This difference is probably the result of a lack of dissolved oxygen in the interstitial

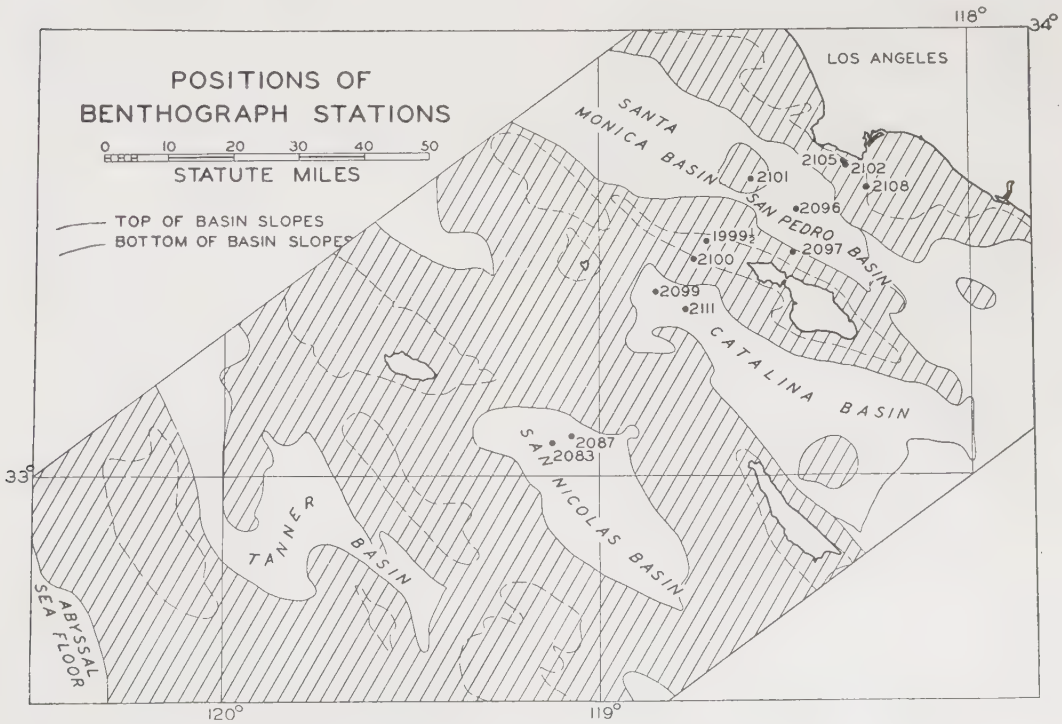

FIG. 2. Geographical distribution of benthograph stations in basins of southern California.

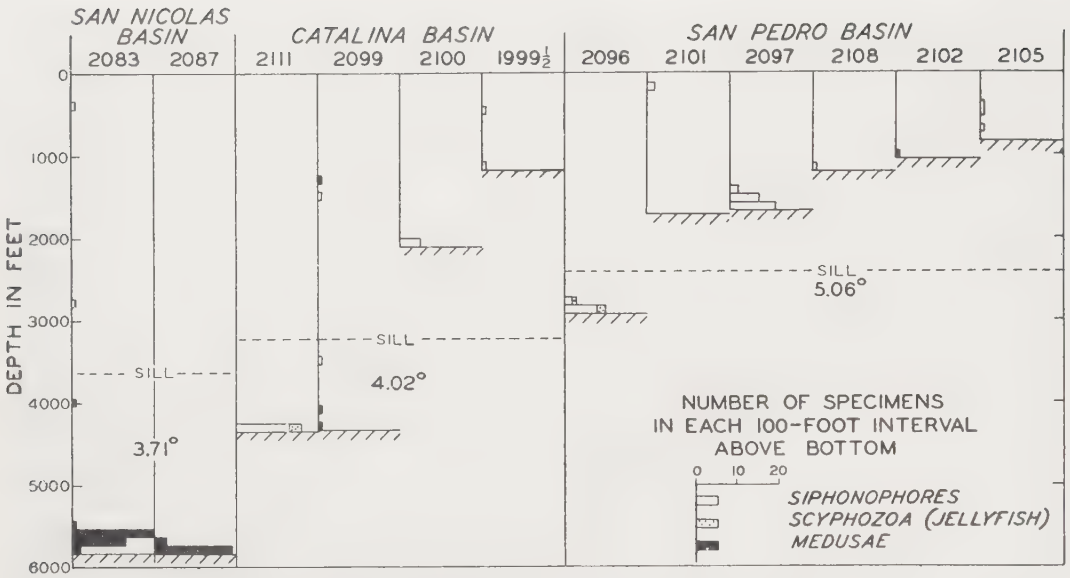

FIG. 3. Depths at each benthograph station at which bathypelagic coelenterates were photographed. Bars show numbers of individuals at 100-foot depth intervals above the bottom.

waters of the sediment in San Pedro Basin, which makes the sediment uninhabitable for many small burrowing animals such as worms but provides no barrier to larger animals living above the bottom and making temporary incursions into it. The total content of organic matter in the top few inches of bottom sediments is high, averaging about 10.3, 9.1, and 7.6 per cent for San Nicolas, Catalina, and San Pedro Basins, respectively (Emery and Rittenberg 1952). Thus, food is far more concentrated at the bottom than at any depth in the water column.

The fact that the siphonophores and scyphozoans are most abundant just above the floor of San Pedro Basin, which is nearly barren of benthonic animals, indicates that they are feeding on bathypelagic animals not visible in the photographs. The tentacles of coelenterates are provided with stinging organs to paralyze prey, and a short closed gut (the coel-enteron) is adapted to rapidly digest concentrated foods. It can be assumed, therefore, that bathypelagic medusae resemble other coelenterates in their food requirements. Whether the latter consist of deep water fishes or some other animals has not been established. However, the sediments have revealed the presence of small deep-water scallop mollusks, one of which is *Cyclopecten*, of which the delicate valves occur in conspicuous numbers; this harbors a commensal serpulid annelid, *Protis* (Hartman 1955b: 52). Both of these animals are believed to be bathypelagic and filter-feeding, and may in turn be fed upon by coelenterates. The food of the medusae in the lowest parts of San Nicolas and Catalina Basins might consist of some of the animals known to exist in or on the sediments.

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APPENDIX

STATION LIST

The following station list of the underwater photographs gives the geographical location and other descriptive data, together with the kinds of animals that have been recognized. Depths are presented in chronological order.

STATION 1999½ Nov. 5, 1950. Lat. 33° 31.4′; Long. 118° 42.5′.
Bottom is green mud at 1171 feet and its temperature 7.2° C.
Ridge northwest of Santa Catalina Island.
470 feet—1 trachyline medusa
? feet—swarm of squids
1160 feet—bathyphysid siphonophore

STATION 2083 Nov. 18, 1951. Lat. 33° 04.5′; Long. 119° 07.1′.
Bottom is green mud at 5840 feet and its temperature 3.7° C.
San Nicolas Basin.
5500 feet—1 trachyline medusa
5610 feet—1 trachyline medusa
5614 feet—1 trachyline medusa
5640 feet—4 trachyline medusae
5670 feet—6 trachyline medusae
5700 feet—2 trachyline medusae
5823 feet—1 trachyline medusa
5749 feet—1 trachyline medusa
5710 feet—1 trachyline medusa
5671 feet—1 trachyline medusa
5623 feet—2 trachyline medusae
5589 feet—14 trachyline medusae (Plate 1, D)
3990 feet—1 trachyline medusa (Plate 2, B)
2751 feet—1 abylid siphonophore
380 feet—1 siphonophore with zig-zag tail (Plate 3, D)

STATION 2087 Nov. 19, 1951. Lat. 33° 05.5′; Long. 119° 04.2′.
Bottom is green mud at 5839 feet and its temperature 3.7° C.
San Nicolas Basin.
5640 feet—1 trachyline medusa
5690 feet—2 trachyline medusae
5755 feet—1 trachyline medusa
5758 feet—1 trachyline medusa
5761 feet—2 trachyline medusae
5763 feet—2 trachyline medusae
5770 feet—1 trachyline medusa
5773 feet—3 trachyline medusae
5780 feet—1 trachyline medusa
5785 feet—1 trachyline medusa
5792 feet—2 trachyline medusae
5812 feet—1 trachyline medusa
5816 feet—1 trachyline medusa
5780 feet—1 trachyline medusa
5765 feet—1 trachyline medusa (Plate 1, C)
5760 feet—1 trachyline medusa (Plate 1, B)
5810 feet—1 trachyline medusa
5830 feet—1 trachyline medusa
5820 feet—1 trachyline medusa
5780 feet—1 trachyline medusa
5800 feet—1 trachyline medusa (Plate 1, A)
5805 feet—1 trachyline medusa
5800 feet—1 trachyline medusa
5830 feet—1 trachyline medusa
5820 feet—1 trachyline medusa
5820 feet—1 trachyline medusa
5790 feet—1 trachyline medusa
5820 feet—1 trachyline medusa
5830 feet—1 trachyline medusa
5830 feet—1 trachyline medusa
5830 feet—1 trachyline medusa
5810 feet—1 trachyline medusa

STATION 2096 March 29, 1952. Lat. 33° 35.4′; Long. 118° 28.1′.
Bottom is green mud at 2921 feet and its temperature 5.1° C.
San Pedro Basin.
2916 feet—3 abylid siphonophores (Plate 3, C) and 2 campanulate scyphozoans
2915 feet—1 bathyphysid siphonophore (Plate 4, A)
2910 feet—1 abylid siphonophore
2890 feet—1 bathyphysid siphonophore
2910 feet—2 abylid siphonophores
2814 feet—1 abylid siphonophore
2806 feet—1 campanulate scyphozoan and 1 abylid siphonophore (Plate 3, E) and 1 bathyphysid siphonophore
2878 feet—1 abylid siphonophore
2735 feet—1 abylid siphonophore
1125 feet—1 slender object with bulb at either end (not identified)

STATION 2097 March 29, 1952. Lat. 33° 29.6′; Lat. 118° 29.0′.
Bottom is green mud at 1663 feet and its temperature 6.4° C.
Slope of San Pedro Basin.
1510 feet—2 abylid siphonophores
1528 feet—1 abylid siphonophore
1549 feet—2 abylid and 1 bathyphysid siphonophores (Plate 3, A, B)

1568 feet—3 abylid siphonophores
1585 feet—1 abylid siphonophore
1616 feet—1 abylid and 1 bathyphysid siphonophore
1631 feet—1 abylid siphonophore
1648 feet—2 abylid and 1 bathyphysid siphonophores
1647 feet—1 abylid siphonophore
1660 feet—1 abylid siphonophore
1465 feet—1 bathyphysid siphonophore
1375 feet—1 abylid and 1 bathyphysid siphonophore

STATION 2099 March 30, 1952. Lat. 33° 24.0′; Long. 118° 50.9′.

Bottom is green mud at 4330 feet and its temperature 4.0°C.
Catalina Basin.
4115 feet—1 trachyline medusa
3475 feet—1 abylid siphonophore
1445 feet—1 abylid siphonophore
1225 feet—1 trachyline medusa in sound-scattering layer (Plate 2, A)

STATION 2100 March 30, 1952. Lat. 33° 29.2′; Long. 118° 45.5′.

Bottom is green mud sloping between 2065 and 2099 feet and its temperature is 5.5° C.
Slope of Catalina Basin.
2080 feet—1 bathyphysid siphonophore (Plate 4, C)
2060 feet—1 bathyphysid siphonophore (Plate 4, B)
2040 feet—1 abylid siphonophore
2054 feet—1 abylid siphonophore
2080 feet—1 abylid siphonophore

STATION 2101 March 30, 1952. Lat. 33° 39.9′; Long. 118° 35.5′.

Bottom is green mud at 1714 feet and its temperature 6.1° C.
San Pedro Basin near sill from Santa Monica Basin.
1706 feet—a prawn
170 feet—2 abylid siphonophores

STATION 2102 March 30, 1952. Lat. 33° 41.2′; Long. 118° 20.2′.

Bottom is green mud sloping between 957 feet to more than 1045 feet and its temperature is about 8.0° C.
Slope of San Pedro Basin.
1045 feet—1 *Gonionemus*-like medusa (Plate 2, C)

STATION 2105 April 9, 1952. Lat. 33° 41.3′; Long. 118° 20.2′.

Bottom is green mud at 840 feet and its temperature is about 8.5° C.
Top of slope of San Pedro Basin.
660 feet—1 abylid siphonophore and a dumbbell-shaped unidentified object (out of focus)
510 feet—1 abylid siphonophore
400 feet—1 abylid siphonophore

STATION 2108 April 20, 1952. Lat. 33° 38.4′; Long. 118° 16.7′.

Bottom is green mud sloping between 870 and 1410 feet and its temperature is about 8.0° C.
San Pedro Sea Valley in slope of San Pedro Basin.
1200 feet—1 abylid siphonophore near bottom
1381 feet—a spindle-shaped object, not identified

STATION 2111 April 29, 1952. Lat. 33° 22.4′; Long. 118° 47.2′.

Bottom is green mud at 4373 feet and its temperature 4.0° C.
Catalina Basin.
1225 feet—1 trachyline medusa
4313 feet—1 trachyline medusa
4314 feet—2 trachyline medusae
4315 feet—2 trachyline medusae
4315 feet—2 trachyline medusae
4316 feet—1 trachyline medusa
4316 feet—1 trachyline medusa
4370 feet—7 trachyline medusae
4370 feet—1 scyphozoan medusa
4360 feet—1 scyphozoan medusa (Plate 2, D)
4360 feet—1 scyphozoan medusa

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